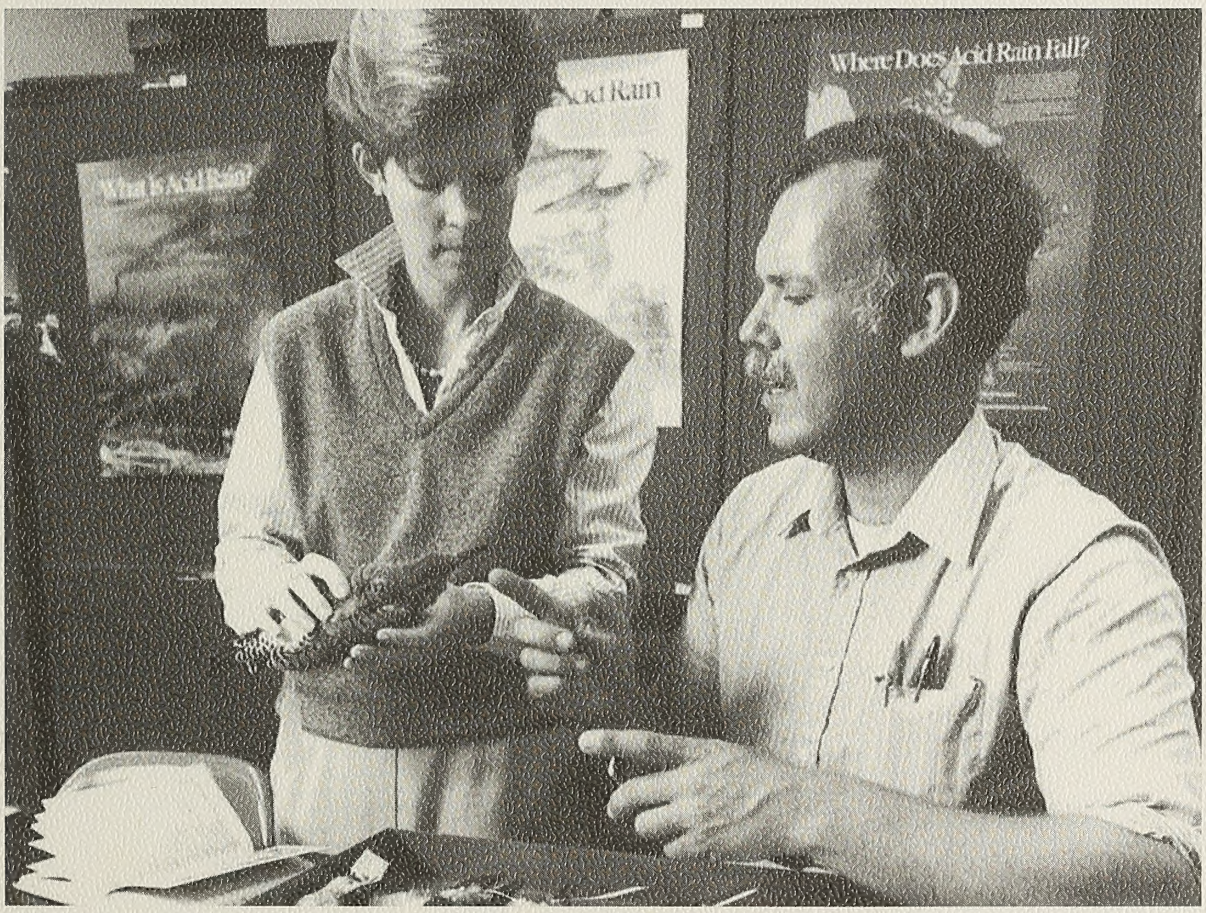
Q
11
.S85X
NH

ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 118 **Number 3**


What is Acid Rain?
Acid Rain
Where Does Acid Rain Fall?

SMITHSONIAN INSTITUTE, COPY 1
ACQUISITIONS/EXCHANGE NMNH 25
SMITHSONIAN INST 10TH ST AND CONSTITUTION AVE NW
WASHINGTON DC 20013
14

118(3) 139-202 (2019 **December 2019**

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

2018–2019 OFFICERS
David Ginsburg, *President*
Lisa Collins, *Vice-President*
Edith Read, *Recording Secretary*
Amber Brown, *Treasurer*
Kristy Forsgren, *Corresponding Secretary*
Daniel J. Pondella II and Larry G. Allen, *Editors - Bulletin*
Brad R. Blood, *Editor - Newsletter*
Shelly Moore, *Webmaster*

SMITHSONIAN
JAN 08 2019
LIBRARIES

ADVISORY COUNCIL
Ralph Appy, *Past President*
Jonathan Baskin, *Past President*
Brad R. Blood, *Past President*
John H. Dorsey, *Past President*
Julianne Kalman Passarelli, *Past President*
John Roberts, *Past President*

BOARD OF DIRECTORS

2016-2019	2017-2020	2018-2021
Mia Adreani	David Ginsburg	Kimo Morris
Julianne Passarelli	Gordon Hendler	Shelly Moore
Edith Read	Shana Goffredi	Ann Bull
Danny Tang	Amber Brown	Kristy Forsgren
Lisa Collins	Gloria Takahashi	Ted Stankowich

Membership is open to scholars in the fields of natural and social sciences, and to any person interested in the advancement of science. Dues for membership, changes of address, and requests for missing numbers lost in shipment should be addressed to: Southern California Academy of Sciences, the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

CATEGORY	E-BULLETIN ONLY	PAPER AND E-BULLETIN
Professional	$60	$80
Student*	$10	$30
Institutional	$135	$135
Life	$2,500	$2,500

* *Must provide proof of student status with application*

Fellows: Elected by the Board of Directors for meritorious services.

The Bulletin is published three times each year by the Academy. Submissions of manuscripts for publication and associated guidelines is at SCASBULLETIN.ORG. All other communications should be addressed to the Southern California Academy of Sciences in care of the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Date of this issue 23 December 2019

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

Bull. Southern California Acad. Sci.
118(3), 2019, pp. 139–157

Experimental Elucidation of the Life Cycle of *Rhinebothrium urobatidium* (Cestoda: Rhinebothriidea) from the Round Stingray (*Urobatis halleri*: Myliobatiformes) to First and Second Intermediate Hosts

Ralph G. Appy,[1]* Shana K. Goffredi,[2] Bruno Pernet,[3] and Carin Latino[1]

[1] *Cabrillo Marine Aquarium, 3720 Stephen M. White Drive, San Pedro, CA 90731*
[2] *Occidental College, Dept of Biology, 1600 Campus Rd, Los Angeles, 90041*
[3] *Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Blvd, Long Beach, CA 90840*

Abstract.—The life cycle of the cestode *Rhinebothrium urobatidium*, whose final host is the round stingray, *Urobatis halleri*, includes a copepod as the first intermediate host and small benthic fishes as second intermediate hosts. Hexacanth embryos within nonoperculate, untanned eggs collected from round stingray developed in the tidepool copepod *Tigriopus californicus* into caudate procercoids with an apical organ/sucker and cercomer, and rarely, bothridia. The procercoids, which developed in the body cavity within a membrane, adhered to the copepod intestine, were infective to arrow gobies, *Clevelandia ios*, within 15 d of exposure at 21°C. When infected copepods were fed to arrow gobies, procercoids developed into nonlacunate plerocercoids each bearing individually retractable bothridia and an apical sucker. Within 10 d of exposure to the second intermediate host, the larvae had migrated up the bile/cystic duct into the gall bladder, where they developed bothridia similar to those of adult worms. Between 30 to 51 d post-infection in the goby, plerocercoids approached the size of larvae found in natural infections, and the scolex became morphologically similar to that of adult worms from round stingrays. Only presumptive filiform microtriches (filitriches) were present on procercoids while both filitrichs and spiniform microtriches (spinitrichs) were present on plerocercoids. Identification of plerocercoids from experimental infections as those of *R. urobatidium* was confirmed through morphology of the scolex and using cytochrome c oxidase I sequences. The experimental transmission of *R. urobatidium* to first and second intermediate hosts provides improved understanding of the transmission and ontogeny of shark tapeworms. The biological characteristics of *U. halleri,* with its diverse parasite fauna, provide significant opportunities to examine the biology of an array of elasmobranch tapeworm taxa.

The Rhinebothriidea comprises approximately 24 genera and 143 species of eucestode tapeworms found as adults in the spiral intestine of batoid elasmobranchs (Caira and Jensen 2014; Ruhnke et al. 2017; Coleman et al. 2019a; Coleman et al. 2019b). While there are numerous reports of larval stages (metacestodes) of members of the Rhinebothriidea from various invertebrate and fish intermediate hosts (Chambers et al. 2000; Caira and Reyda 2005; Jensen and Bullard 2010), there are no publications that describe the experimental transmission of these parasites from egg to adult worm (Caira and Jensen 2014).

---

* Corresponding author: r.appy@cox.net

This lack of information on the Rhinebothriidea and marine cestode life cycles in general is surprising considering the abundance and diversity of these worms. The sparsity of information on marine cestode life cycles is an impediment to a more complete understanding of tapeworm ontogeny and evolution (Beveridge 2001) and to a better understanding of the important role parasites play in the food chain of many ecosystems (e.g., see Lafferty et al. 2006).

During studies on fish and macroinvertebrate parasites of Anaheim Bay in Southern California, plerocercoids with a scolex resembling that of *R. urobatidium* (Young, 1955) (see Appy and Dailey 1977) were found in the gall bladder and bile duct of small benthic fish. Larvae were particularly abundant in arrow gobies, *Clevelandia ios*, (Jordon and Gilbert, 1882) and shadow gobies, Quietula y-cauda (Jenkins and Evermann, 1889) collected in four man-made tidal ponds. *Rhinebothrium urobatidium* is also one of the most abundant parasites of the round stingray, *Urobatis halleri* (Cooper, 1863), which is seasonally present in large numbers in the same tidal ponds (Jirik and Lowe 2010) where we observed plerocercoids in small benthic fishes. The purpose of this study is to describe the morphogenesis of the tapeworm in its intermediate hosts, and to confirm the identity of these plerocercoids as *R. urobatidium* with morphological features and DNA sequence data.

Materials and Methods

Round stingrays were collected at a number of collecting events from 2016 to 2018 in Anaheim Bay (hook and line, beach seine), Seal Beach (hook and line), San Diego Bay (hook and line), Long Beach Harbor (otter trawl), and Two Harbors, Catalina Island (by spear), California. A survey of fish parasites was conducted in Anaheim Bay in 2013 using an otter trawl, beach seine and minnow traps. In addition, small benthic fish examined for infection with *R. urobatidium* were collected in Anaheim Bay tidal ponds by beach seine in the fall of 2018. Arrow and cheekspot gobies, *Ilypnus gilberti* (Eigenmann and Eigenmann, 1889) (Gobiidae) used for experimental infections were collected in Cabrillo Salt Marsh, Los Angeles Harbor. For morphological and sequence data comparison with larvae obtained experimentally, adult *R. urobatidium* were collected from round stingrays at multiple localities in Southern California (see above) and plerocercoids were from gobies collected in Anaheim Bay.

Gravid proglottids of *R. urobatidium* taken from round stingrays were placed in seawater in small (25 ml) plastic cups, and, following expulsion of eggs, were removed from the cups. Eggs were rinsed with several changes of seawater. Eggs were examined with a compound microscope to confirm their morphology as that of *R. urobatidium*. Eggs were maintained in seawater at 21°C with daily seawater changes until use in experimental infections, which usually occurred within 3 d.

Experimental infections with *R. urobatidium* were carried out using the tidepool copepod *Tigriopus californicus* (Baker, 1912) (Harpacticoidea) obtained from a colony maintained at the Cabrillo Marine Aquarium as a first intermediate host, and wild caught arrow and cheekspot gobies as second intermediate hosts. None of 23 gobies examined at the time of collection in Cabrillo Salt Marsh were infected with *R. urobatidium*. At a subsequent collection, 1 of 31 gobies was infected with a single *R. urobatidium*. In addition, infections were attempted using ostracods [tentatively identified as *Cyprides beaconensis* (Leroy, 1943)] collected in tidal pools in San Diego Bay as a first intermediate host and commercially available mosquitofish [*Gambusia affinis* (Baird and Girard, 1854)] as a second intermediate host.

Eggs of *R. urobatidium* were pipetted into 25 ml plastic cups containing copepods or ostracods. After 8 hours, copepods and ostracods were placed in a loosely covered 125 ml plastic cup in an incubator at 21°C. Copepods were fed Nanno 3600 (Instant Algae) daily and ostracods were fed finely ground marine fish pellets once a week. Evaporation from the cups was compensated by adding distilled water. Five to ten copepods were examined for larvae of *R. urobatidium* at each sampling event over a 20 d period. Ostracods were examined 15 d post exposure (dpe) to eggs of *R. urobatidium*.

At 15 dpe two to five copepods experimentally infected with *R. urobatidium* were fed to both gobies and mosquitofish, that had been placed individually in 125 ml plastic cups. After eight hours, all copepods had been consumed and gobies and mosquitofish were removed from the individual cups and each species placed in a liter glass bowl at 21°C. Gobies and mosquitofish were fed ground dry marine aquarium fish pellets and frozen copepods. Gobies were examined at irregular intervals or at times when a fish was found moribund such as occurred at 51 dpe. Both arrow and cheekspot gobies were used in experimental infections although measurement data presented herein came only from plerocercoids removed from arrow gobies. All fish examined in the lab were euthanized using ~250 mg/l of Tricaine (MS222).

Larvae isolated from copepods and dissected from gobies were observed live under a petroleum jelly-rimmed coverslip and then heat killed using the flame of a match prior to measuring. Measurements of plerocercoids were made on worms heat-killed prior to placing the coverslip to avoid effects of compression by the coverslip and attachment/flattening of bothridia adhering to the slide/coverslip. Measurements, drawings, and photographs were made using a Wild M12 compound microscope fitted with an optical graticule, drawing tube, and a Canon EOS 60e digital camera. Hand drawings were scanned and inked using Adobe Illustrator. The contrast and brightness of photographs and micrographs were sometimes enhanced using Adobe Photoshop. Unless stated otherwise, measurements are given in micrometers (μm).

Selected specimens used for scanning electron microscopy (SEM) included: adult worms from round stingray, plerocercoids from naturally and experimentally infected arrow goby, and procercoids from experimentally infected *T. californicus*. Specimens were placed directly into fixative or were heat killed with steaming hot water, fixed in 1.25% glutaraldehyde, post-fixed in 1% osmium tetroxide, dehydrated in an ethanol series, critical point dried using $C0_2$, and mounted on stubs. Specimens were coated with gold/palladium using an Emitech K550x sputter coater (Quorum Technologies, Ltd, Kent, UK) and imaged using a Hitachi S3000N variable pressure SEM (Hitachi, Troy, MI). For histology, approximately 15 infected copepods were fixed in Alcohol-Formalin-Acetic Acid (AFA), embedded in mass in paraffin, sectioned at 6–8 μm, and stained with hematoxylin and eosin. The morphology of adult worms was examined using a compound microscope by placing worms on a microscope slide and compressing slightly with a coverslip. This allowed accurate counting of loculi and testes.

Specimens obtained from experimental trials and from wild caught round stingrays were fixed in 95% ethanol for molecular analyses. Total genomic DNA was extracted from these samples using the Qiagen DNeasy Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions. A 572 base pair region of the cytochrome c oxidase I (COI) gene was amplified via the polymerase chain reaction (PCR) using Cestoda-specific primers nLCO (5′-TTT ACT YTR GAY CAT AAG CGT-3′), and BEN-5 (5′-AAG CAG AAC CAA TTT ACG ATC-3′), according to Reyda and Marques (2011). Successful PCR reactions, determined via electrophoresis, were cleaned using MultiScreen HTS plates (Millipore

Corporation, Bedford, MA) and sequenced via Laragen, Inc. (Los Angeles, CA). Alignments to close relatives were performed in Sequencher v4.10.1 and distance matrices (Jukes-Cantor model) were created using Geneious v8.0.2. Sequences of *R. urobatidium* obtained from experimental infections were compared to *R. urobatidium*, *Ruptobothrium ditesticulum* (Appy and Dailey, 1977) Coleman et al., 2019 and *R. gravidum* Friggens and Duszynski, 2005 from wild caught *U. halleri*, collected during the current study. COI sequences generated during this study are available via GenBank (Acc. #MN416032-MN416047).

Tapeworm ontogenetic and morphological terminology generally follows that of Chervy (2002) for larval stages (but see Discussion), (Caira et al. 1999) for scolex attachment organs, Conn and Swiderski (2008) for embryonic envelopes, Chervy (2009) for microtriches; Jensen and Bullard (2010) for larval types, and Hilliard (1960) and Bylund (1975) for hexacanth hooks. Miller and Lea (1972) was used to identify fishes.

Results

In the 2013 survey of fish parasites in Anaheim Bay, 75.6% (N = 41) of round stingray were found to be infected with 1 to 53 adult *R. urobatidium*. The only other rhinebothriidean species present included *R. gravidum* (85.4%) and *R. ditesticulum* (26.8%). Presumptive *R. urobatidium* plerocercoids were found in the gall bladder and bile ducts of several species of small benthic fish including 22.7% (N = 22) of longjaw mudsuckers (*Gillichthys mirabilis* Cooper, 1864) 23.1% (N = 26) of arrow and shadow gobies and 6.3% (N = 32) of staghorn sculpins (*Leptocottus armatus* Girard, 1854). These larvae were absent in topsmelt [*Atherinops affinis* (Ayres, 1860)] (N = 30), California killifish (*Fundulus parvipinnis* Girard, 1854) (N = 37), shiner surfperch (*Cymatogaster aggregata* Gibbons, 1854) (N = 16), yellowfin goby [*Acanthogobius flavimanus* (Temminck and Schlegel, 1845)] (N = 9), and barred sand bass (*Paralabrax nebulifer* (Girard, 1854)) (N = 60*)*. *Rhinebothrium urobatidium* was particularly common in the tidal ponds where in 2013, 100% of arrow goby were infected with 2 to 54 worms. In the fall of 2018, 93% of 43 arrow and cheekspot gobies collected in Anaheim Bay tidal ponds were found to be infected with 1 to 57 plerocercoids per fish.

Apolytic gravid proglottids of *R. urobatidium* (Fig. 1A) in the spiral intestine of round stingrays were initially distinguished/segregated from other gravid proglottids by a combination of moderate size relative to the gravid proglottids of other tapeworm species, uniform white appearance, a smooth surface and an indistinct midbody genital pore. Identfication as *R. urobatidium* was confirmed by examining egg morphology using a compound microscope. When placed in seawater, eggs extruded from an opening midway along the proglottid (Fig. 1A). Eggs of *R. urobatidium* taken directly from gravid proglottids were nonoperculate and enclosed by a transparent outer coat with a robust gradually tapering terminally rounded filament extending from one pole (Figs. 1B, 2A). Within this clear membrane the hexacanth embryo was surrounded by inner and outer envelopes. Expelled eggs held in seawater did not attach to one another or become tanned. Embryos were active within the envelopes. Hexacanth hooks were not uniform in size or shape (Table 1, Fig. 2B). The medial (third) pair were longer than the lateral (first) or medio-lateral (second) pairs and had a more recurved blade tip, and the mediolateral pair were shorter than the medial pair and had a wider handle and blade. The lateral pair was the most delicate with a gently curved blade tip and thin handle.

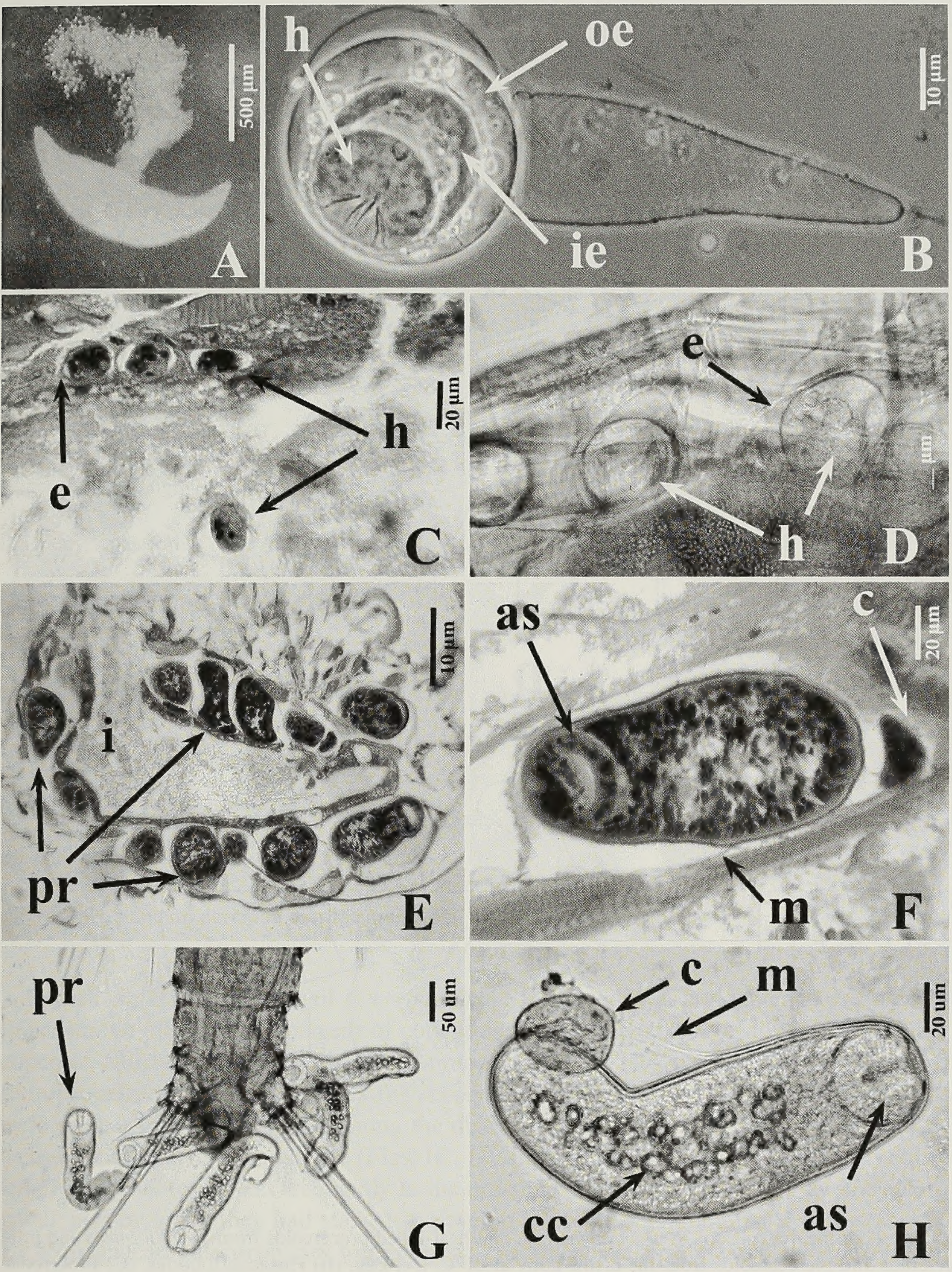


Fig. 1. Photographs of the development of *R. urobatidium* in *T. californicus,* held at 21°C. (A) Gravid proglottid expelling eggs. (B) Egg containing hexacanth embryo under coverslip pressure. (C) Hexacanth embryo in copepod intestinal lumen and in hemocoel at 8 hours post-exposure. (D) Hexacanth embryo within an envelope in copepod hemocoel. (E) Procercoids within a membrane in the copepod hemocoel at 10 d post-exposure (dpe). (F) Proceroid within a membrane at 10 dpe. (G) Procercoids isolated from a copepod at 14 dpe. (H) Mature procercoid within a membrate at 14 dpe. Abbreviations: as – apical sucker, c – cercomer, cc – calcareous corpuscles, h – hexacanth embryo, ie – inner envelope, m–membrane, oe – outer envelope, pr – procercoid.

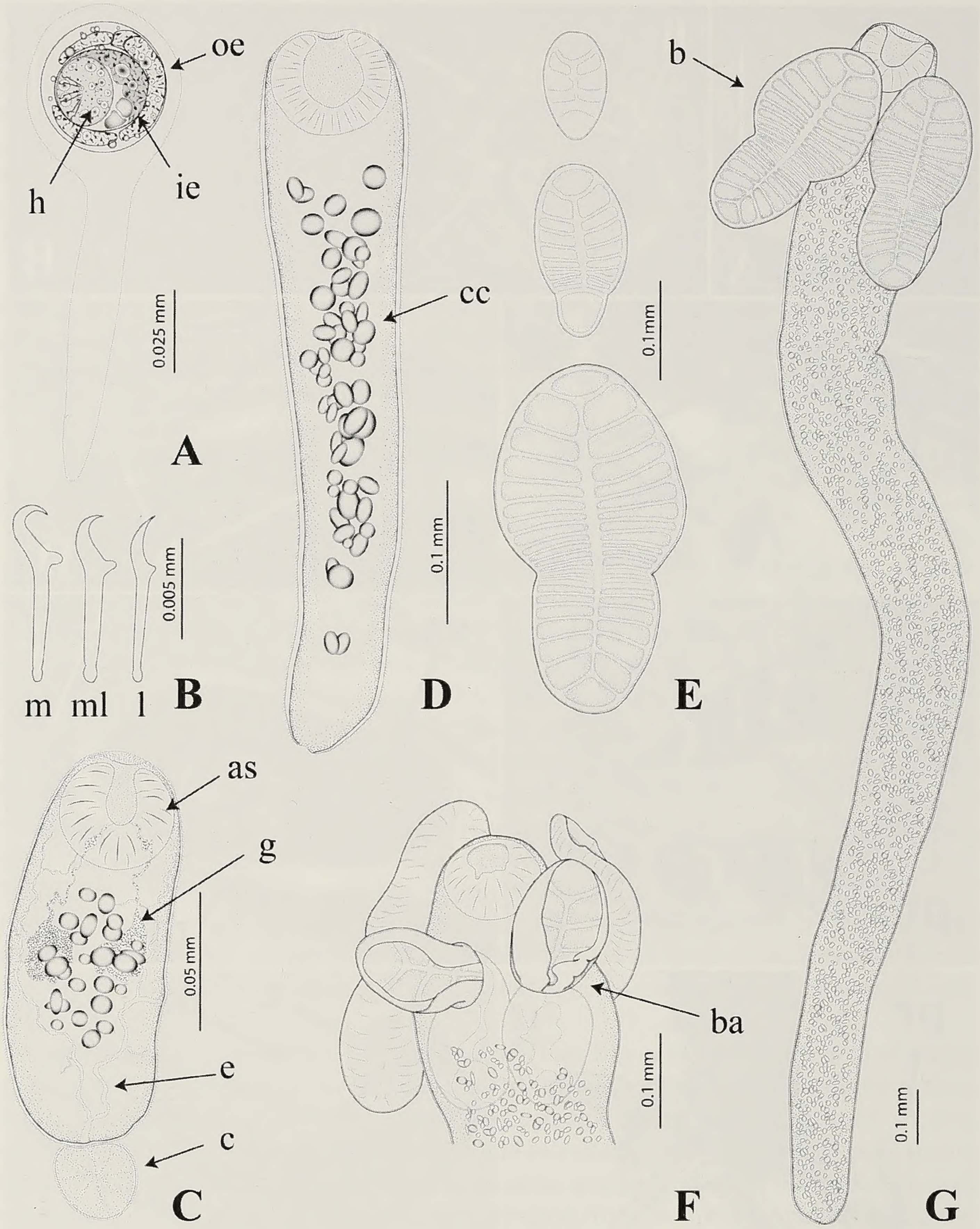


Fig. 2. Line drawings of *R. urobatidium* egg, and heat-killed procercoids from *T. californicus* and procercoids and plerocercoids from the arrow goby at 21°C. (A) Egg. (B) Hexacanth hooks. (C) Procercoid with cercomer at 10 d post-exposure (dpe). (D) Procercoid from arrow goby at 8 dpe. (E) Stages in bothridial development of the plerocercoid. (F) Plerocercoid with bothridia partially retracted. (G) Habitus of plerocercoid at 60 dpe. Abbreviations: as - apical sucker, b - bothridia, ba - bothridial aperture, c - cercomer, cc - calcareous corpuscles, g - gland cells and ducts, e - excretory system, ie - inner envelope, l - lateral hook, m - medial hook, ml - mediolateral hook, oe - outer envelope.

Table 1. Morphometrics in micrometers (μm)* of eggs and hexacanth larvae of *R. urobatidium*.

Parameter	
Number	10
Total length	144 ± 7.0 129–157
Maximum width	48 ± 2.3 45–51
Filament length	92 ± 6.3 79–103
Filament width	14 ± 1.0 12–15
Outer envelope length	40 ± 1.8 37–42
Outer envelope width	35 ± 1.7 32–37
Inner envelope length	29 ± 1.4 27–32
Inner envelope width	23 ± 2.3 20–25
Hexacanth length	22 ± 1.2 21–24
Hexacanth width	16 ± 1.2 14–18
Embryonic Hook Length	
Lateral Pair	8.2 ± 0.14 7.9–8.4
Medio-lateral Pair	8.3 ± 0.19 8.1–8.7
Medial Pair	9.0 ± 0.27 8.6–9.5

* Mean ± standard deviation over the range.

Experimental transmission of *R. urobatidium* to copepods was conducted in excess of 20 times, and in all cases 100 percent of copepods became infected with up to 48 larvae per copepod. Mortality of copepods was common in the first days of infection. Two attempts to infect ostracods were not successful. At eight hours post-exposure, hexacanth embryos were present in copepod tissues lining the digestive tract, where they were surrounded by a clear space and thin membrane (Figs. 1C, D). Larvae penetrated the gut along its entire length but were found less frequently in the urosome (hindgut). As larvae grew they elongated, and by 5 dpe they had started to develop a cercomer and an apical organ/sucker. By 8 dpe calcareous corpuscles were present, the apical sucker appeared fully developed, and the cercomer was oval and connected to the body proper (Figs. 1F, G, H; 3A, B) by a narrow isthmus (Fig. 3C). Procercoids were clustered around the copepod digestive tract and surrounded by a thin membrane (Figs. 1E, F, H; 3B, C). Hexacanth hooks were not visible on the cercomer, but were occasionally observed in the posterior body of mature procercoids. While growth of some larvae continued through at least 20 dpe (Fig. 4A), elongation slowed following 8 dpe and by 11 dpe some larvae were near the maximum size of larvae examined at 20 dpe. Glandular cells were present in the anterior midbody of the procercoid, with ducts extending into the area of the apical sucker (Fig. 2C). The excretory

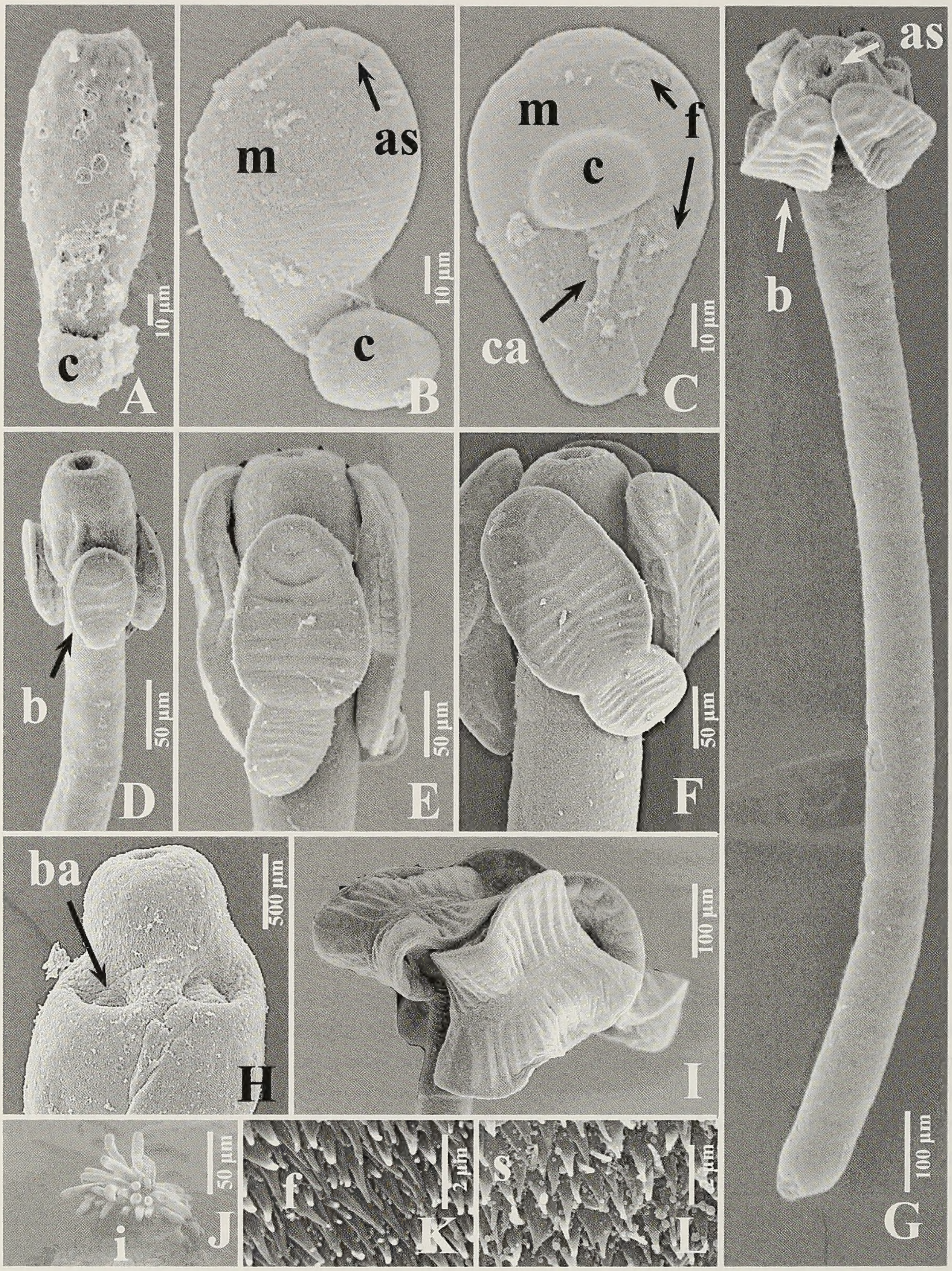


Fig. 3. Scanning electron micrographs of *R. urobatidium* in experimental (A–E, G–H, J–K) and natural infections (F, I). A. Procercoid from *T. californicus* at 15 d post-exposure (dpe). B, C. Procercoid from *T. californicus* with enclosing membrane at 15 dpe. D. Plerocercoid from arrow goby at 30 dpe. E, G. Plerocercoid from arrow goby at 51 dpe. F, H. Plerocercoid from natural infection of arrow goby. I. Adult scolex of specimens from round stingray. J. Bodies of plerocercoids extending from bile duct into the intestinal lumen of arrow goby. K. Procercoid microtriches at 15 dpe. L. Plerocercoid microtriches at 51 dpe. Abbreviations: as - apical sucker, b - bothridium, ba - bothridial aperture, c - cercomer, ca - cercomer attachment, f - filithriches, i - intestine, m - membrane, s - spinitriches.

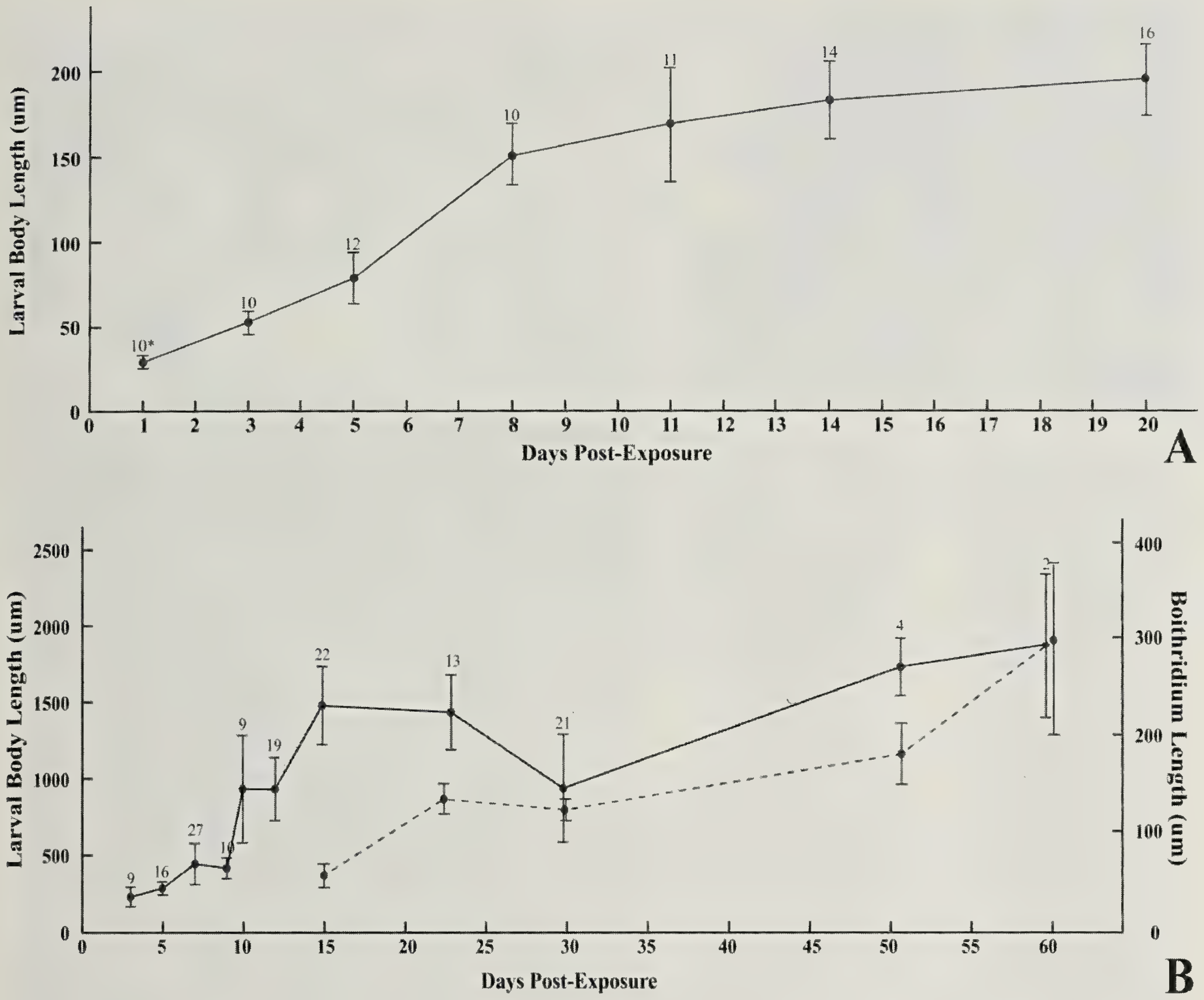


Fig. 4. Growth of *R. urobatidium* in intermediate hosts held at 21°C: A. Procercoids in *T. californicus.* B. Procercoids/plerocercoids in arrow goby. Solid line is total length of larvae while dashed line is change in length of bothridia.

system consisted of a posterior common duct, which bifurcated in two lateral branches extending into the anterior end of the larvae. During development in the copepod, larvae usually did not move freely within the hemocoel, but adhered to the external surface of the digestive tract (Fig. 1E). No obvious bothridial development occurred within 20 dpe. However, one of two larvae present in a copepod at 30 dpe had developed rudimentary bothridia and was moving in the hemocoel.

Gobies experimentally infected with *R. urobatidium* procercoids from copepods harbored 11 to 44 larvae. At 5 dpe, procercoids with the apical sucker, but without a cercomer (Fig. 2D), were present between villi in the anterior intestine of experimentally infected gobies (Fig. 5A). By 7 dpe some larvae, which had increased in length (Fig. 4B), were present in the bile duct and gall bladder (Fig. 5B); those in the gall bladder had attached to its inner wall by the apical sucker. Bothridia began forming in some larvae by 10 dpe as indistinct anterior swellings (Fig. 5C), and subsequently became septate oval bothridia, which developed anterior and posterior lobes as they increased in size (Figs. 2E; 3D, E, G; 5D). Septa at the anterior end formed first, with septa increasing in number and definition as the infection progressed (Fig. 2E). By 51 to 60 dpe, 36 to 38 loculi were present in the longer plerocercoids (Figs. 2E, G; 3G; 5E). During development, the anterior bothridial lobe was larger than the posterior lobe, and more loculi were present in the anterior lobe than in

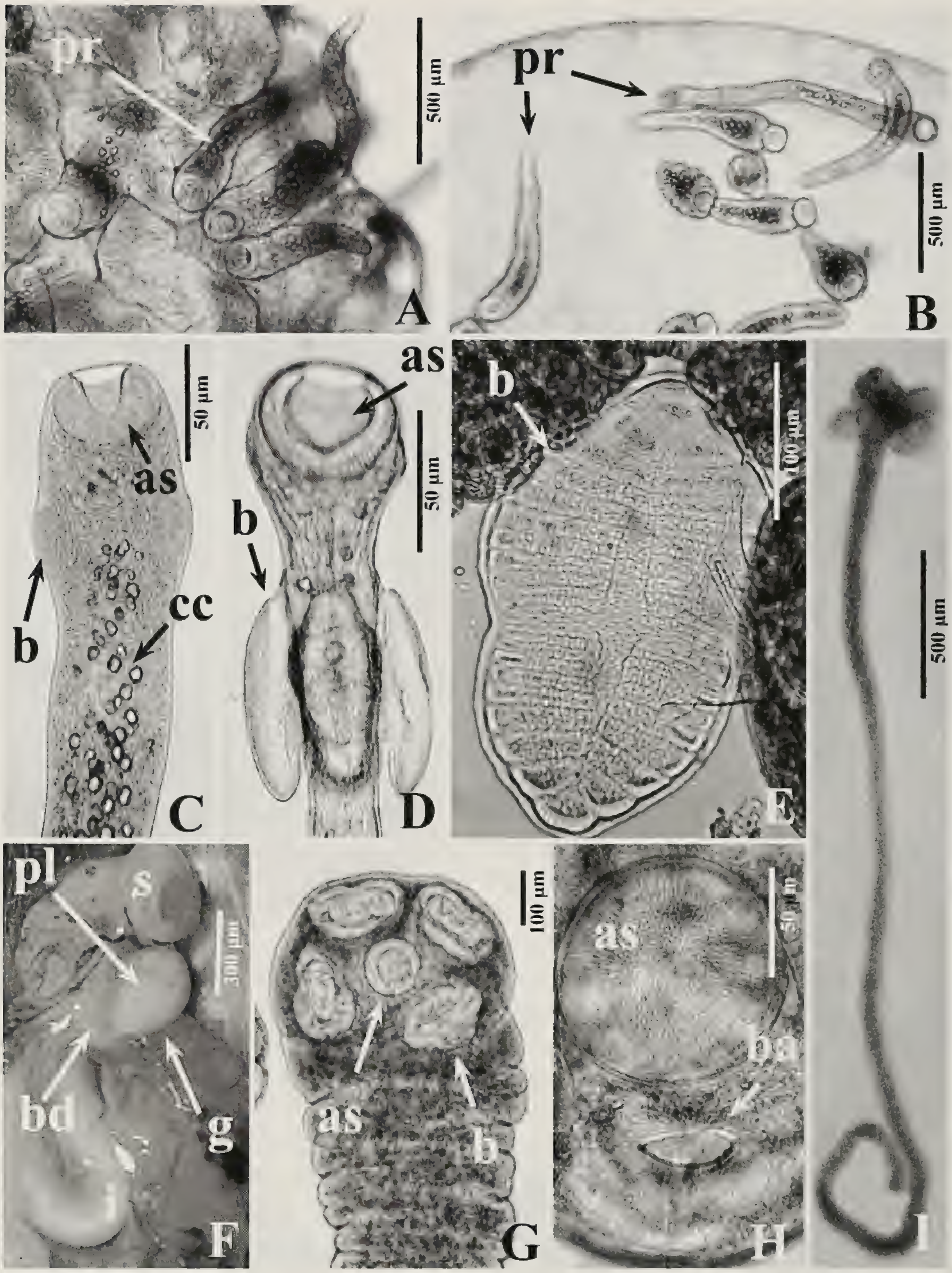


Fig. 5. Photographs of *R. urobatidium* larvae in arrow goby held at 21°C: (A) Procercoids among the goby intestinal villi. (B) Procercoids attached to the inner wall of the gall bladder at 10 d post-exposure (dpe). (C) Procercoid beginning to differentiate into a plerocercoid at 15 dpe. (D) Plerocercoid with developing bothridia at 30 dpe. (E) Developed bothrium attached to coverslip at 60 dpe. (F) Digestive tract of goby with plerocercoids in the gall bladder and bile duct. (G) Plerocercoid with bothridia and apical sucker retracted at 60 dpi. (H) Aperture of a retracted bothridium. I. Extended plerocercoid from a naturally infected arrow goby. Abbreviations: as - apical sucker, b - bothridia, ba - bothridial aperture, bd - bile duct, cc - calcareous corpuscles, g - gall bladder, i - intestine, im - inner envelope, oe - outer envelope, m - microtriches, pr - procercoid, pl - plerocercoid, s - stomach.

Table 2. Morphometrics in micrometers (µm)[*] of larval stages of *R. urobatidium* in copepods (*T. californicus*) and arrow gobies.

Parameter	Procercoid (20 dpe)[†]	Plerocercoid (51–60 dpe)[†]	Plerocercoid Natural Infection
Number	14	6	7
Body length	196 ± 16.3 167–223	1778 ± 377.9 1338–2414	2808 ± 922.5 1237–3906
Body width	68 ± 7.1 59–85	151 ± 38.9 89–203	704 ± 308.9 238–1125
Apical sucker length	40 ± 2.6 35–44	92 ± 16.8 75–116	75 ± 14.9 46–94
Apical sucker width	41 ± 2.5 36–44	98 ± 11.9 83–116	105 ± 27.3 47–128
Cercomer length	34 ± 6.6 21–46	-	-
Cercomer width	36 ± 4.4 30–43	-	-
Bothridium length		229 ± 81.1 170–387	327 ± 60.6 213–382
Bothridium width		130 ± 45.3 98–220	101 ± 75.4 85–190
Number of loculi		32–38	34–40

[*] Mean ± standard deviation over the range.

[†] dpe = days post-exposure.

the posterior lobe (Figs. 2E; 3E). In heat-killed specimens, the shape and reflexion of the scolex/bothridia was similar to that in heat-killed plerocercoids and adult worms from natural infections (Figs. 3G, I). By 51 to 60 dpe, some plerocercoids approached the length of larvae present in naturally infected gobies (Table 2). Plerocercoids were densely packed with calcareous corpuscles and had excretory canals similar to those seen in the procercoid. In heavy experimental and natural infections, the gall bladder and the bile duct were congested with plerocercoids (Fig. 5F) and in one case, the posterior portion of the larvae extended out of the bile duct into the intestine (Fig. 3J). In some cases, procercoids (larvae without bothridial development) were still present in the bile duct and gall bladder as late as 30 dpe. The bodies of plerocercoids were highly elastic (Fig. 5I), and the bothridia and apical sucker could individually be retracted into the scolex (Figs. 2F; 3H; 5G, H). The pedicel retracted into the scolex followed by the posterior portion of bothridium and then the anterior portion. Plerocercoids viewed in the gall bladder of fish invariably were attached to the inner bladder wall with the apical sucker and with bothridia retracted. In both experimental and natural infections, developed plerocercoids were present in the biliary system but not in the intestine. No plerocercoids that could be attributed to a different morphotype were found in the bile/cystic duct or gall bladder of gobies although plerocercoids of other tapeworms (believed to be *Acanthobothrium* spp. and *Parachristianella* sp.) were present in the lumen of the posterior intestine and rectum. Mosquitofish did not become infected in two trial exposures.

Presumptive filitriches were present on procercoids (Fig. 3K) but absent on the cercomer. In plerocercoids, filitriches were present adjacent to the apical sucker, and spinitriches were present on the corpus sometimes mixed with filitriches (Fig. 3L). Microtriches became sparse toward the posterior of the plerocercoid.

Table 3. Genetic relationship of *R. urobatidium* (*R.u.*) from experimental infections with natural infections of *R. urobatidium*, at different localities, *R. gravidum* (*R.g.*) and *R. ditesticulum* (*Ru.d.*) based on mitochondrial cytochrome oxidase 1. Numbers represent the difference in base pairs in a 465 base pair region.

				Ru. d.	***R.g.***	***R. urobatidium***					
Species	Stage	N[*]	Locality[†]	adult AB	adult LAH	adult LBH	adult SB	adult SDB	plero. AB	plero. 30 dpe	plero. 60 dpe
Ru. d.	adult	1	AB	–	123	117–118	117–118	117–118	117	117	117
R. g.	adult	1	LAH		–	117	117–119	117–118	118	117	117
R. u.	adult	4	LBH			**0–2**	1–3	0–1	1–2	0–1	0-1
	adult	2	SB				**3**	1–3	1–2	1–2	1-2
	adult	4	SDB					**0–2**	1–2	0–1	0-1
	plero.	1	AB						–	1	1
	plero.	2	30							**0**	0
	plero.	1	60								–

[*] N = number of specimens sequenced.

[†] AB = Anaheim Bay, LAH = Los Angeles Harbor, LBH = Long Beach Harbor, SB = Seal Beach, SDB = San Diego Bay; plero. = plerocercoid. dpe = days post exposure.

Cytochrome c oxidase I sequences of experimental plerocercoids were nearly identical to those from plerocercoids and adult *R. urobatidium* from natural infections, with only 1–3 basepair differences out of a total 465-bp region, compared to 117–119 bp mismatch with other rhinebothriidean species (Table 3).

Discussion

The three-host life cycle of *R. urobatidium* includes a first intermediate host copepod where a caudate procercoid with an apical organ/sucker and cercomer develops, a second intermediate host small benthic fish in which a nonlacunate plerocerocoid bearing individually retractable bothridia and apical sucker develops in the biliary system, and the final host, the round stingray. Eggs of *R. urobatidium* include inner and outer envelopes, which are likely homologous with embryonic envelopes recognized by Conn and Swiderski (2008). The outermost clear membrane with a single rounded process may be the outer coat formed in some cestodes (Conn and Swiderski 2008). Other rhinebothriidean species including *R. abaiensis* Healy, 2006 (Healy 2006) and *R. gravidum* and *R. ditesticulum* (pers. obs.) have a transparent outer coat, although the eggs of these species all possess a process extending from each end of the egg. Other tapeworm species have similar outer coats (e.g. *Proteocephalus* spp. of the order Onchoproteodephalidea (Scholz 1999). The size and shape of these eggs is certainly a microecological adaptation that enhances transmission (Jarecka 1961) either by providing buoyancy, being attractive/refractive, and/or by mimicking a particular food (e.g. phytoplankton) of the first intermediate host.

The development of a procercoid with a cercomer and apical organ/sucker is a common ontogenetic feature among the Cestoda (Freeman 1973, Jarecka 1975, Chervy 2002), but within the Rhinebothriidea this stage has only been described for *Pseudanthobothrium* Baer, 1956 (Jarecka and Burt 1984). Unlike in *R. urobatidium*, the cercomer of *Pseudanthobothrium* spp. contains large refractile bodies. In addition, the body (protoscolex) of *Pseudathobothrium* is enclosed with a clear membrane within which the larva moves freely and separately from the cercomer (Jarecka and Burt 1984). In contrast, a clear membrane observed in *R. urobatidum* surrounds the entire procercoid, including the cercomer, and the body of the procercoid is directly attached to the cercomer. In *R. urobatidum* the movement of the procercoid is constrained within the membrane, perhaps by virtue of its attachment to the cercomer.

Among acetabulate fish tapeworms, development of a procercoid with an apical sucker and a cercomer, as in *R. urobatidium*, is also found in *Acanthobothrium olseni* (Mudry and Dailey 1971), *A. hispidum* (Riser 1956), and similar to initial development in species of *Proteocephalus* Wineland, 1858 (Scholz 1999). In most *Proteocephalus* spp. the formation of cercomer and apical sucker is quickly followed by the development of four suckers similar to what is found in the adult worms (Scholz 1999). In contrast, *R. urobatidium* did not develop bothridia in the first 20 d in the copepod, and larvae without bothridia fed to gobies at 15 dpe, developed bothridia similar to the adult worm. Thus in *R. urobatidium* reared in *T. californicus*, the development of bothridia is not required in order to infect the second intermediate host as it apparently is in *Proteocephalus*. The pattern in *R. urobatidum* is more similar to that in the bothriate cestodes such as some bothriocephalideans or diphyllobothriideans, in which the procercoid does not develop an adult-like scolex until it enters the second intermediate fish host (Freeman 1973).

The presence of microtriches on procercoids has been observed in other cestode orders (Davydov et al. 1995). While not studied in detail herein, a transition of microthrix type from procercoid to plerocercoid of *R. urobatidium* has been reported for other tapeworms (Hopkins and Charles 1969). Such a transition is not surprising in light of general ontogenetic tegumental changes that occur in other tapeworm species (Davydov et al. 1995).

The membrane surrounding the procercoid of *R. urobatidium* appears to be of parasite rather than host origin and similar membranes have been observed in other cestode species. Invertebrate immune responses typically involve a cellular response and encapsulation (van der Veen and Kurtz 2002; Rowley and Powell 2007). Such responses were not evident in *T. californicus* infected with *R. urobatidium*. In contrast, ultrastructural and *in vitro* studies have variably described a surface coat in the spathebothriidean *Cyathocephalus truncates* (Pallas 1781) (Okada 1990), an electron-translucent fibrillar secretion around the procercoid of the bothriocephalid *Triaenophorus nodulosus* (Pallas, 1781) (Davydov et al. 1995), a surface filamentous coat in the caryophyllidea *Archigete*s *sieboldi* Leuckart, 1878 (Poddubnaya et al. 2003), and an outer surface or outer layer in the diphyllobothriidean Schistocephalus solidus (Müller 1776) (Jakobsen et al. 2012; Marwaha et al. 2013). The membrane/layer sometimes described as carbohydrate (Jacobson and Doyle 1996) or shed outer surface (Jakobsen et al. 2012) has been purported to help the parasite evade the immune responses of the invertebrate intermediate host (Hammerschmidt and Kurtz 2005) or to provide protection from enzymatic action when the procercoid is passing through the vertebrate host digestive tract (Kurtz and Franz 2003; Marwaha et al. 2013). An ultrastructural/cytochemical study would be needed to better compare the membrane found in *R. urobatidium* with those found surrounding the procercoids of these other tapeworms. Absence of bothridial development in *R. urobatidium* in the copepod may also be related to the presence of this membrane. This is supported by our observation of a single larva of *R. urobatidium* with bothridia moving freely in the copepod hemocoel at 30 dpe. In addition, at least rudimentary bothridia are present in larvae of *R. gravidum* and *A. parvinuncinatum,* which move freely in the hemocoel of *T. californicus* (pers. obs.). This may suggest that conditions in the copepod hemocoel trigger or allow development of bothridia.

The presence or absence of bothridia in the larvae in the first intermediate host may also be related to the trophic demands of transmission. In *Proteocephalus* spp., development of acetabula/scolex in the first intermediate host precedes subsequent development to an adult in the digestive tract of the final host in a usual two-host life cycle (Scholz 1999). In acetabulate fish tapeworms in a three-host cycle, such as *R. urobatidium*, the absence of bothridial development may be related to subsequent location of the larva in the second intermediate host; e.g., bothridia may be an impediment to larval parasites that migrate into ducts (e.g. *R. urobatidium*) or the body cavity [e.g., Type 5 larva of Chambers et al. (2000) and *R. ditesticulum* (pers. obs.)] of the second intermediate host. In any case, while the ontogenetic stages (procercoid and plerocercoid/merocercoid) of acetabulate tapeworms appear similar across taxa, the timing of larval morphogenesis from one to the other in the first intermediate host appears to be variable and likely a species-specific adaptation to trophic requirements of transmission.

The plerocercoid of *R. urobatidium* conforms to Jensen and Bullard's (2010) Type VII, which has an apical sucker and four stalked bothridia that are individually and totally retractable into the scolex. This general type of larva has been reported from the digestive system of a number of fish species from the Great Barrier Reef (Chambers 2000) and in the Gulf of Mexico (Jensen and Bullard 2010). The larval worms described by Brooks and Brothers (1997) from arrow goby and the shadow goby, *Quietula y-cauda* (Jenkins and Evermann, 1889) (Gobiidae) in San Diego Bay, California are most likely *R. urobatidium*. Small benthic fish in Anaheim Bay are commonly infected with *R. urobatidium,* especially in the man-made tidal ponds. The heavy use of these tidal ponds by gestating round stingray in the late summer and fall (Jirik and Lowe 2012) evidently provides a focus of infection of small benthic fish with *R. urobatidium*. The occurrence of rhinebothriidean larvae in fish is not always consistent with the feeding habits of final hosts, which consume few fish (Jensen and Bullard 2010). This is also true for *R. urobatidium*, in which the round stingray's diet consists of only 7.5% fish (Babel 1967).

While the presence of larval shark tapeworms in the gall bladder and bile/cystic duct of a fish host does not appear to be a common occurrence (e.g. see Jensen and Bullard 2010) larvae that might be attributed to *Rhinebothrium* or related taxa have been reported from the biliary system of fish (Linton 1897, 1905; Chandler 1935; Overstreet 1968; Jensen 2009). In tapeworms of groups other than elasmobranchs, acystic larvae of *Valipora* spp. (Cyclophyllidea: Gryporhynchidae), parasites of birds, are also found in the gall bladder of bony fishes (Jarecka 1970; Scholz and Salgado-Maldonado 2001). Larval helminths exploit intermediate host tissues to avoid the gut, maximize their growth, and minimize mortality (Chubb et al. 2009; Parker et al. 2009a, b). The specialized location of *R. urobatidium* in the biliary system, which might seem to be an inhospitable environment, would provide the benefits of being in host tissues or body cavities while avoiding the need to penetrate host tissues. In particular, *R. urobatidium* plerocercoids in the biliary system avoid energy expenditure associated with withstanding gut peristalsis, possibly avoid host immune response due to minimal host/parasite contact, and evidently find adequate nutrition to significantly increase their size. The protruding of the posterior ends of larvae into the intestinal lumen could be a means to obtain nutrition (Fig. 3J) although this was only observed in heavy experimental infections of the arrow goby.

The larvae of *R. urobatidium*, like those of at least some other *Rhinebothrium* species (see Jensen and Bullard 2010), possess neither evaginated bothridia (plerocercoid) nor an invaginated scolex (merocercoid). Instead, bothridia of *R. urobatidium* are individually retractable; they are withdrawn, without invagination of the bothridia, into the scolex. In discussing larval cestode terminology Chervy (2002) recognized the difficulty in the use of scolex retraction and invagination as a feature in defining larval types but felt it may be a useful feature. Other authors have also noted difficulty in assigning a designation to the bothridia of plerocercoids (Rocka 2003; Guagliardo et al. 2009). While larval *R. urobatidium* from gobies do not appear to fit neatly into the definition of a plerocercoid or merocercoid it seems premature to create new or resurrect terminology in light of the absence of transmission and ultrastructural studies on the thousands of shark tapeworm metacestodes. Therefore, we have utilized the term plerocercoid, which is consistent with the terminology used by Jensen and Bullard (2010) for similar larvae.

The number of bothridial loculi present in the plerocercoid of *R. urobatidium* approaches or reaches the number of loculi in adult worms (Table 2; Appy and Dailey 1977), suggesting that in regions where the local elasmobranch tapeworms are known, plerocercoids of *Rhinebothrium* may be attributed to an adult form and thus a species based on the bothridial morphology of the plerocercoid. In addition to morphological similarity between experimental plerocercoids and adult worms, and plerocercoids from natural infections, mitochondrial DNA sequence data confirmed the finding that among rhinebothriidean tapeworms commonly found as adults in round stingray (i.e., *R. gravidum* and *R. ditesticulum*) in Anaheim Bay and Southern California, larvae from experimental infections are those of *R. urobatidium* (Table 3). Similarly Laskowski and Rocka (2014) found fewer than five base pair differences in COI sequence between plerocercoids from marbled rockcod, *Notothenia rossii* Richardson, 1844, and the onchoproteodephalidean *Oncobothrium antarticum* Wojciechowska, 1990 from the skate *Bathyraja eatonii* (Gunther 1876), a finding also confirmed with lsrDNA, which not surprisingly showed no molecular differences. In contrast, Jensen and Bullard (2010) found that congeners of some shark tapeworms may have identical COI sequences and recommended caution in identification of larvae or adults to species using COI. However, even absent genetic data, *R. urobatidium* can be distinguished from other rhinebothriidean tapeworms occurring in round stingray. *Ruptobothrium ditesticulum*, which is relatively scarce in round stingray in Anaheim Bay, has bothridia comprising two separate lobes, very large gravid proglottids and eggs with filaments at both poles. The bothridia of *R. gravidum* are not indented/lobed, their gravid proglottids have crenulated surface, prominent genital atrium and eggs have filaments at both poles. *Rhinebothrium urobatidium* exhibits substantial growth in both intermediate hosts. Procercoid growth was asymptotic and reached growth arrest at larval maturity (GALM) (Ball et al. 2008; Parker et al. 2009a) between 8 and 11 dpe at 21°C (Fig. 4). In contrast, while the morphological development and bothridial growth of the plerocercoids proceeded sequentially, growth in length of the larvae was quite variable. This is likely a fixation artifact related to highly contractile plerocercoid, and a less-than-optimum experimental design including the examination of only a single goby at each sampling point, and possible over-infection of small (~2 cm) goby hosts. In particular, extremely high intensity of infection has been shown to cause delayed development in the intermediate host (Benesh 2010). The goby examined at 30 dpe in the present study (Fig. 4) was infected with 44 larvae, which completely filled the gall bladder and greatly expanded the width of the bile duct. It should also be noted that experimental plerocercoids at 51 to 60 dpe did not reach the maximum size of larvae from natural infections (Table 2). Additional experimental studies will be necessary to better determine when growth arrest occurs in the plerocercoid and at what point in development plerocercoids become infective to the final host.

While recent years have seen a rise in morphological/taxonomic and phylogenetic information on elasmobranch tapeworms (e.g. Caira and Jensen 2014; Caira et al. 2014; Caira and Jensen 2017), there are few experimental/ultrastructural studies on any of the nine orders of elasmobranch tapeworms. This is in contrast to the significant advances in experimental and ultrastructural studies of some mammalian and avian tapeworms (e.g. Michaud et al. 2006; Hammerschmidt and Kurtz 2009) including the sequential in vitro development of the procercoid and pleroceroid of *Schistocephalus solidus* (Jakobson et al. 2012). The present study experimentally confirms the identity of elasmobranch tapeworm plerocercoids found in small benthic fish as *R. urobatidium,* and for the first time describes morphogenesis of larval stages from first to second intermediate hosts. However, it still falls short of documenting the exact transmission that occurs in nature. It seems clear that *R. urobatidium* has a three-host life cycle, but the species of the natural first invertebrate (copepod) intermediate host(s) of *R. urobatidium* is still unknown, and worms have yet to be experimentally transmitted to the final host to determine time to maturity and longevity. Finding copepods infected with *R. urobatidium* in the marine environment is a difficult undertaking (although not impossible – see Marcogliese 1995), and use of wild-caught round stingrays for experimental studies is not feasible since regardless of size or locality of capture, they are invariably infected with a menagerie of tapeworm species. We are currently studying the use of oral anthelminthics to remove digestive tract parasites from wild-caught stingrays and husbandry of stingrays born live in captivity to allow more complete transmission studies. Round stingray is a particularly good host for experimental studies since it is well-studied locally (Babel 1967; Hoisington and Lowe 2005; Vaudo and Lowe 2006; Mull et al. 2008; Plank et al. 2010; Jirik and Lowe 2012; Lyons et al. 2017), is abundant and easily caught in shallow waters where large congregations of rays result in foci of parasite transmission, is small and relatively easy to maintain/feed in captivity, and above all, it has a diverse tapeworm fauna including representatives from a number of tapeworm orders (Rhinebothriidea, Trypanorhyncha, Diphyllidea, and Onchoproteocephalidea).

Acknowledgments

Collection of round rays and gobies was made possible under Scientific Collecting Permit Nos. 13105 and 1527 issued to the first author and the Cabrillo Marine Aquarium, respectively, by the California Department of Fish and Wildlife. Mr. Kirk Gilligan and Richard Nye, U. S. Fish and Wildlife Service, provided a Special Use Permit for collection of stingrays and gobies at Anaheim Bay and Ms. Eileen Maher, Port of San Diego provided access to collect stingrays in San Diego Bay. Mr. Jeff Landesman provided access to the copepod colony at Cabrillo Marine Aquarium. Drs. Kady Lyons and Dennis Noesen provided help in collection of stingrays. Michael Appy provided paraffin-sectioned and stained material. SEM was carried out at the Natural History Museum of Los Angeles County courtesy of Dr. Regina Wetzer and with assistance of Adam Wall. Dr. Ian Beveridge kindly reviewed an early draft of this manuscript. Special thanks to Dr. Murray Dailey for the introduction to shark worms, and remembrance of the late Dr. Leokadia "Lena" Jarecka, who provided the senior author with an appreciation for tapeworm ontogeny and the skill involved in using a pipette to capture individual copepods from a five-gallon bucket. Thank you to the peer reviewers, whose detailed comments contributed significantly to the quality of this manuscript.

Literature Cited

Appy R.G. and M.D. Dailey. 1977. A new species of *Rhinebothrium* (Cestoda: Tetraphyllidea) and redescription of three rhinebothriate species from the round stingray, *Urolophus halleri* Cooper in Southern California. BSCAS, 54(6):116–127.

Babel, J.S. 1967. Reproduction, life history, and ecology of the round stingray, *Urolophus halleri* Cooper. Fish Bull., Calif. Depart. Fish Game, 137:105–120.

Ball, M.A., G.A. Parker and J.C. Chubb. 2008. The evolution of complex life cycles when parasite mortality is size- or time-dependent. J. Theor. Biol., 253:202–214.

Banesh, D.P. 2010. Developmental inflexibility of larval tapeworms in response to resource variability. Int. J. Parasitol., 40:487–497.

Beveridge, I. 2001. The use of life cycle characters in studies of the evolution of cestodes. Pp. 250-256 in Interrelationships of the Platyhelminths (D.T.J. Littlewood and R.A. Bray eds.). Syst. Assoc. Spec. Vol. Ser. 60. Taylor and Francis, London.

Brooks, D.R. and E.B. Brothers 1977. Helminths of three species of goby (Pisces: Gobiidae) from Mission Bay, San Diego. J. Parasitol., 60(6): 1062–1063.

Bylund, G. 1975. The taxonomic significance of embryonic hooks in four European *Diphyllobothrium* species (Cestoda, Diphyllobothriidae). Acta Zool. Fen., 142, 23 pp.

Caira, J.N., K. Jensen and C.J. Healy. 1999. On the phylogenetic relationships among tetraphyllidean, lecanicephalidean and diphyllidean tapeworm genera. Syst. Parasitol. 42:77–151.

———, F.N. Reyda. 2005. Eucestoda (true tapeworms) Pp. 92–104 In Marine Parasitology (K.Rohde ed.). CSIRO Publishing, Collingwood.

——— and K. Jensen. 2014. A digest of elasmobranch tapeworms. J. Parasitol., 100(4):373–391.

———, K. Jensen, A. Waeschenbach, P.D. Olson and D.T.J. Littlewood 2014. Orders out of chaos-molecular phylogenetics reveals the complexity of shark and stingray tapeworm relationships. Int. J. Parasitol., 44:55–73.

— and K. Jensen 2017 (eds.). Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. Univ. Kansas Nat. Hist. Mus. Spec. Publ. No. 25, 463 pp.

Chambers, C.B., T.H. Cribb and M.K. Jones. 2000. Tetraphyllidean metacestodes of teleosts of the Great Barrier Reef, and the use of *in vitro* cultivation to identify them. Folia Parasitol., 47: 285–292.

Chandler, A.C. 1935. Parasites of fishes in Galveston Bay. Proc. U. S. Nat. Mus., 83: 123–157.

Chervy, L. 2002. The terminology of larval cestodes or metacestodes. Syst. Parasitol., 52:1–33.

——— 2009. Unified terminology for cestode microtriches: a proposal from the International Workshops on Cestode Systematics in 2002–2008. Folia Parasitol., 56(3):199–230.

Chubb, J.C., M.A. Ball and G.A. Parker. 2009. Living in intermediate hosts: evolutionary adaptations in larval helminths. Evol. Parasitol., 26(2):93–102.

Coleman, G.M., I. Beveridge and R.A. Campbell. 2019a. New species of *Rhinebothrium* Linton, 1890 (Cestoda: Rhinebothriidea) parasitic in Australian stingrays (Elasmobranchii: Batoidea). Syst. Parasitol 96:23–49.

—, I. Beveridge, and R.A. Campbell. 2019b. New genera, species and records of rhinebohriidean cestodes (Platyhelminthes) parasitic in Australian stingrays (Elasmobranchii: Batoidea). Syst. Parasitol. 96:347–368.

Conn, D.B and Z. Swiderski 2008. A standardized terminology of the embryonic envelopes and associated developmental stages of tapeworms (Platyhelminthes: Cestoda). Folia Parasitol., 55:42–52.

Davydov, V.G., J.V. Korneva and B.I. Kuperman 1995. The development of the tegument in ontogenesis of *Triaenophorus nodulosus* (Cestoda: Pseudophyllidea). Folia Parasitol., 42:269–279.

Freeman, R.S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. Adv. Parasitol., 11:481–557.

Guagliardo, S., D. Tanzola, C. Schwerdt and N. Galeano. 2009. Host-parasite relationships between *Porichthys porosissimus* (Pices) and cestode larvae of the *Scolex* group. Helminthologia, 46(3): 162–167.

Hammerschmidt, K. and J. Kurtz 2005. Surface carbohydrate composition of a tapeworm in its consecutive intermediate hosts: Individual variation and fitness consequences. Int. J. Parasitol., 35:1499–1507.

——— and J. Kurtz. 2009. Ecological immunology of a tapeworm's interaction with its two consecutive hosts. Adv. Parasitol. (J.P. Webster ed.), Chapter 5, 68:111–137.

Healy, C.J. 2006. Three new species of *Rhinebothrium* (Cestoda: Tetraphyllidea) from the freshwater whipray, *Himantura chaophraya*, in Malaysian Borneo. J. Parasitol., 92(2):364–374.

Hilliard, D.K. 1960. Studies on the heminth fauna of Alaska. XXXVIII. The taxonomic significance of eggs and coracidia of some diphyllobothriid cestodes. J. Parasitol., 46:703–716.

Hoisington, G., IV and C.G. Lowe. 2005. Abundance and distribution of round stingray, *Urobatis halleri*, near a thermal outfall. Mar. Env. Res., 60:437–453.

Hopkins, C.A. and G. Charles. 1969. Host specificity and rejection of *Schistocephalus solidus*. Parasitology, 59(3):683–690.

Jacobson, R.A. and R.J. Doyle 1996. Lectin-parasite interactions. Parasitol. Today, 12(2):55–61.

Jakobsen, P.J., J.P. Scharsack, K. Hammerschmidt, P. Deines, M. Kalbe and M. Milinski. 2012. In vitro transition of *Schistocephalus solidus* (Cestoda) from coracdium to procercoid and from procercoid to plerocercoid. Exp. Parasitol., 130:267–273.

Jarecka, L. 1961. Morphological adaptations of tapeworm eggs and their importance in the life cycles. Acta Parasitol. Pol., 9(26):409–426.

——— 1970. Life cycle of *Valipora* (Wedl, 1855) Baer and Bona, 1958–1960 (Cestoda: Dilepididae) and the description of cercoscolex – a new type of cestode larvae. Bull. Acad. Pol. Sci. Classe II. Ser. Sci. Biol., 18(2):99–102.

——— 1975. Ontogeny and evolution of cestodes. Acta Parsit. Pol. 23:93–114.

——— and M.D.B. Burt 1984. The cercoid larvae of *Pseudanthobothrium hanseni* Baer, 1956 and *Pseudanthobothrium* sp. (Cestoda, Tetraphyllidea) from experimentally infected harpacticoid copepods. Acta Parasitol. Pol., 24(2):23–26.

Jensen. K. 2009. Cestoda (Platyhelminthes) of the Gulf of Mexico. Pp. 487–522 in Gulf of Mexico – Origins, Waters, and Biota (D.L. Felder and D.K. Camp eds.). Biodivesity. Texas A&M Univ. Press.

Jensen, K. and S.A. Bullard 2010. Characterization of a diversity of tetraphyllidean and rhinebothriidean cestode larval types, with comments on host associations and life cycles. Int. J. Parasitol., 40: 889–910.

Jirik, K.E. and C.G. Lowe 2012. An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. J. Fish Biol., 80(5):1227–1245.

Kurtz, J. and K. Franz. 2003. Evidence for memory in invertebrate immunity. Nature, 425:37–38.

Lafferty, K.D., A.P. Dodson and A.M. Kuris. 2006. Parasites dominate food web links. PNAS, 103: 11211–11216.

Laskowski, Z and A. Rocka 2014. Molecular identification larvae of *Onchobothrium antarcticum* (Cestoda: Tetraphyllidea) from marbed rockcod, *Notothenia rossii*, in Admiralty Bay (King George Island, Antarctica). Acta Parasitol., 59(4):767–772.

Linton, E. 1897. Notes on larval parasites of fishes. Proc. U. S. Nat. Mus., 19:787–824.

——— 1905. Parasites of fishes of Beaufort North Carolina. Bull. U. S. Bur. Fish., 24:321–428.

Lyons, K., A.B. Carlisle and C.G. Lowe 2017. Influence of ontogeny and environmental exposure on mercury accumulation in muscle and liver of male round stingrays. Mar. Env. Res., 130:30–37.

Marcogliese, D.J. 1995. The role of zooplankton in the transmission of helminth parasites to fish. Rev. Fish Biol. Fish. 5:336–371.

Marwaha, J., K.H. Jensen and P.J. Jakobsen 2013. The protection afforded by the outer layer to procercoids of *Schistocephalus solidus* during passage through the stomach lumen of their vertebrate host (*Gasterosteus aculeatus*). Exp. Parasitol., 134(1):12–17.

Michaud, M., M. Milinski, G.A. Parker and J.C. Chubb. 2006. Competitive growth strategies in intermediate hosts: experimental tests of a parasite life-history model using the cestode, *Schistocephalus solidus*. Evol. Ecol., 20(1):39–57.

Miller, D.J. and R.N. Lea. 1972. Guide to the coastal marine fishes of California. State of California, Resources Agency, Dept. Fish and Game. Fish Bull., 157. 235 pp.

Mudry, D. and M.D. Dailey. 1971. Postembryonic development of certain tetraphyllidean and trypanorhynchan cestodes with a possible alternative life cycle for the order Trypanorhyncha. Can. J. Zool., 49(9):1249–1253.

Mull, C.G., C.G. Lowe and K.A. Young. 2008. Photoperiod and water temperature regulation of seasonal reproduction in male round stingrays (*Urobatis halleri*). Integ. Phys., 151(4):717–725.

Okaka, C.E. 1990. Structural studies on the procercoid of *Cyathocephalus truncatus*. Nigerian J. Parasitol., 10:113–120.

Overstreet, R.M. 1968. Parasites of the inshore lizardfish, *Synodus foetens*, from South Florida, including a description of a new genus of Cestoda. Bull. Mar. Sci., 18(2):444–470.

Parker, G.M., M.A. Ball and J.C. Chubb. 2009a. To grow or not to grow? Intermediate and paratenic hosts as helminth life cycle strategies. J. Theor. Biol., 258:135–147.

——— 2009b. Why do larval helminths avoid the gut of intermediate hosts? J. Theor. Biol., 260(3):460–473.

Plank, S.M., C.G. Lowe, K.A. Feldheim, R.R. Wilson, Jr. and J.A. Brussian. 2010. Population genetic structure of the round stingray *Urobatis halleri* (Elasmobranchii: Rajiformes) in southern California and the Gulf of California. J. Fish Biol., 77(2):329–340.

Poddubnaya, L.G., J.S. Mackiewicz and B.I. Kuperman. 2003. Ultrastrucure of *Archigetes sieboldi* (Cestoda: Caryophyllidea): relationship between progenesis, development and evolution. Folia Parasitol., 50:275–292.

Reyda, F.B. and F.P.L. Marques 2011. Diversification and species boundaries of *Rhinebothrium* (Cestoda; Rhinebothriidea) in South American freshwater stingrays (Batoidea; Potamamotrygonidae). PLoS ONE 6(8):e22604.

Riser, N.W. 1956. Early larval stages of two cestodes from elasmobranch fishes. Proc. Helminth. Soc. Wash., 23(2):120–124.

Rocka, A. 2003. Cestodes of the Antarctic fishes. Pol. Polar Res., 24(3–4):261–276.

Rowley, A.F. and A. Powell. 2007. Invertebrate immune systems-specific, quasi-specific, or nonspecific? J. Immun., 179:7209–7214.

Ruhnke, T.R., F.B. Reyda and F.P.L. Marques. 2017. Rhinebothriidea. Pp. 327–348 in Planetary Biodiversity Inventory (2008–2017). Tapeworms from Vertebrate Bowels of the Earth (J.N. Caira, and K. Jensen eds.). Univ. Kansas Nat. Hist. Mus.: Spec. Publ. No. 25.

Scholz, T. 1999. Life cycles of species of *Proteoceophlus*, parasites of fishes in the Palearctic Region: a review. J. Helminthol., 73:1–19.

——— and G. Salgado-Maldonado. 2001. Metacestodes of the family Dilepididae (Cestoda: Cyclophyllidea) parasitizing fish in Mexico. Sys. Parasitol., 49:23–40.

van der Veen, I.T. and J. Kurtz. 2002. To avoid or eliminate: Cestode infections in copepods. Parasitology, 124:465–474.

Vaudo, J.J., and C.G. Lowe 2006. Movement patterns of the round stingray *Urobatis halleri* (Cooper) near a thermal outfall. J. Fish Biol., 68:1756–1766.

Bull. Southern California Acad. Sci.
118(3), 2019, pp. 158–172

Secondary Production of Kelp Bass *Paralabrax clathratus* in Relation to Coastal Eelgrass *Zostera marina* Habitat in a Southern California Marine Protected Area

Richelle L. Tanner,[1] Adam K. Obaza,[2,3] and David W. Ginsburg[1]*

[1] *University of Southern California, Environmental Studies Program, Los Angeles, CA 90089-0156*
[2] *Ocean Associates, Inc., Abingdon, VA 22207*
[3] *Paua Marine Research Group, San Diego, CA 92109*

Abstract.—Seagrasses are an important refuge for fishes and provide ecosystem services worldwide. Along the Pacific Coast, however, quantitative assessments of the ecological role of seagrass habitats with limited anthropogenic impacts are lacking despite their value to resource management. To address these issues, the ecological function of the eelgrass *Zostera marina* Linnaeus in a protected area off Santa Catalina Island, California, USA was quantified using estimates of secondary production in the kelp bass *Paralabrax clathratus* (Girard, 1854). Monthly assessments of *Zostera* structural complexity, as well as the size and abundance of juvenile kelp bass were used to establish a baseline of fish biomass and recruitment associated with *Zostera* habitat. The greatest number of kelp bass was recorded in the summer and fall months and the fewest during the winter and spring. Secondary production in kelp bass (0.1 to 0.59 g m^{-2} mo^{-1}) followed monthly changes in *Zostera* habitat structure throughout the 24-month study period. Seasonal changes in the structural complexity of coastal *Zostera* beds may influence the flow of energy to adjacent reef environments through the transfer of fish biomass. These findings help define the potential role of *Zostera* habitat within the larger context of nearshore coastal ecosystems in the Southern California Bight.

Coastal seagrass beds are an important nursery habitat for fishes and provide a variety of ecosystem services worldwide (Worthington et al. 1992; Heck et al. 2003; Burkholder et al. 2007; Warren et al. 2010; Parsons et al. 2015). Given the significance of this resource, the protection of seagrass habitat has received considerable attention (Coles et al. 2014; Bas Ventín et al. 2015; Schultz et al. 2015). The National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA Fisheries) recognizes seagrasses as habitat areas of particular concern, which are defined as subsets of essential fish habitat under the Pacific Coast Groundfish Fishery Management Plan. Such areas are considered high priorities for conservation and management, and warrant special attention during the regulatory process set forth by the Magnuson Stevens Fishery Conservation and Management Act in 1976. Nevertheless, the management of seagrasses has proven challenging in some areas, particularly those with remote coastlines that are difficult to access, and in other cases due to a paucity of information on seagrass resources altogether (Long and Thom 2001). For example, because of their isolation from the Southern California mainland, the distribution and habitat function of seagrass beds off the California Channel

---

* Corresponding author: dginsbur@usc.edu

Islands are poorly known; this is in contrast to the many long-term studies of shallow rocky reefs and kelp forests from the same region (Engle and Miller 2005).

One of the most common species of seagrass found along the Southern California coast is the eelgrass *Zostera marina* Linnaeus 1753, which forms extensive beds in shallow bays and estuaries with low to moderate current exposure (Dawson and Foster 1982; Engle and Miller 2005). Many of the areas inhabited by *Zostera* are subject to anthropogenic stressors such as dredging, eutrophication and development that decrease the ecological function and stability of these communities (Obaza et al. 2015; Shelton et al. 2017). While studies of *Zostera* beds found in these locations offer information on habitat function in a stressed environment, data from protected areas provide an upper bound of the behavioral response by fishes that are dependent on seagrass as a refuge from predators (Jackson et al. 2001; Gillanders et al. 2003). Such is the case for populations of *Zostera* around the California Channel Islands, which are separated from many of the anthropogenic stressors found along the mainland coast and thus are an ideal location to collect ecological and environmental data (Findlay and Allen 2002; Davis 2005; Mason and Lowe 2010; Saarman and Carr 2013). Of particular interest is information on habitat use and movement patterns of ecologically and economically important populations of reef fishes living in these areas (NOAA 2014). Accordingly, estimates of secondary production are used to quantify the biological benefit of different habitats by accounting for both changes in fish biomass and population parameters that include fish mortality, recruitment, immigration and emigration (DeMartini et al. 1994; Johnson et al. 1994; Love et al. 1996; Faunce and Serafy 2008; Jeong et al. 2009; Kamimura et al. 2011; Yeager et al. 2012; Williams et al. 2013; Claisse et al. 2014).

Here, we compare secondary production in juvenile kelp bass *Paralabrax clathratus* (Girard 1854), a temperate serranid fish, in relation to the three-dimensional (= structural) complexity of *Zostera* habitat in a protected area off Santa Catalina Island, California, USA. *Zostera* forms highly productive beds (Risgaard-Petersen et al. 1998) that function as an important nursery habitat for kelp bass (Mendoza-Carranza and Rosales-Casian 2002; Altstatt et al. 2014), as well as other common and economically important fishes such as rockfish (*Sebastes* sp.) and surfperch (*Embiotocidae*) (Hoffman 1986; Allen et al. 2002). Our findings provide an important baseline of fish biomass and recruitment associated with *Zostera* habitat in the absence of significant anthropogenic impacts. By integrating multiple metrics for evaluating *Zostera* habitat function, such as species use and secondary production, we aimed to improve conservation and management efforts by evaluating the role of *Zostera* habitat in a Southern California marine protected area.

Material and Methods

Study Site and Natural History

Field surveys were conducted monthly from September 2013 to August 2015 in Big Fisherman's Cove (33°26′38.85″N, 118°29′6.86″W) in the Blue Cavern State Marine Conservation Area (SMCA) on Santa Catalina Island, ~35 km off the coast of Southern California, USA (Fig. 1). Neither anchoring nor fishing is allowed in Blue Cavern SMCA, and all commercial and recreational take of marine life is prohibited as outlined by California's Marine Life Protection Act of 1999. The subtidal habitat of Big Fisherman's Cove extends seaward from a northwest facing, boulder and rock cobble beach as a sloping, sandy bottom that steadily descends to depths >35 m that lie towards the center and mouth of the cove. The northeast and southwest borders are comprised of semi-vertical rocky reef (5-20 m depth)

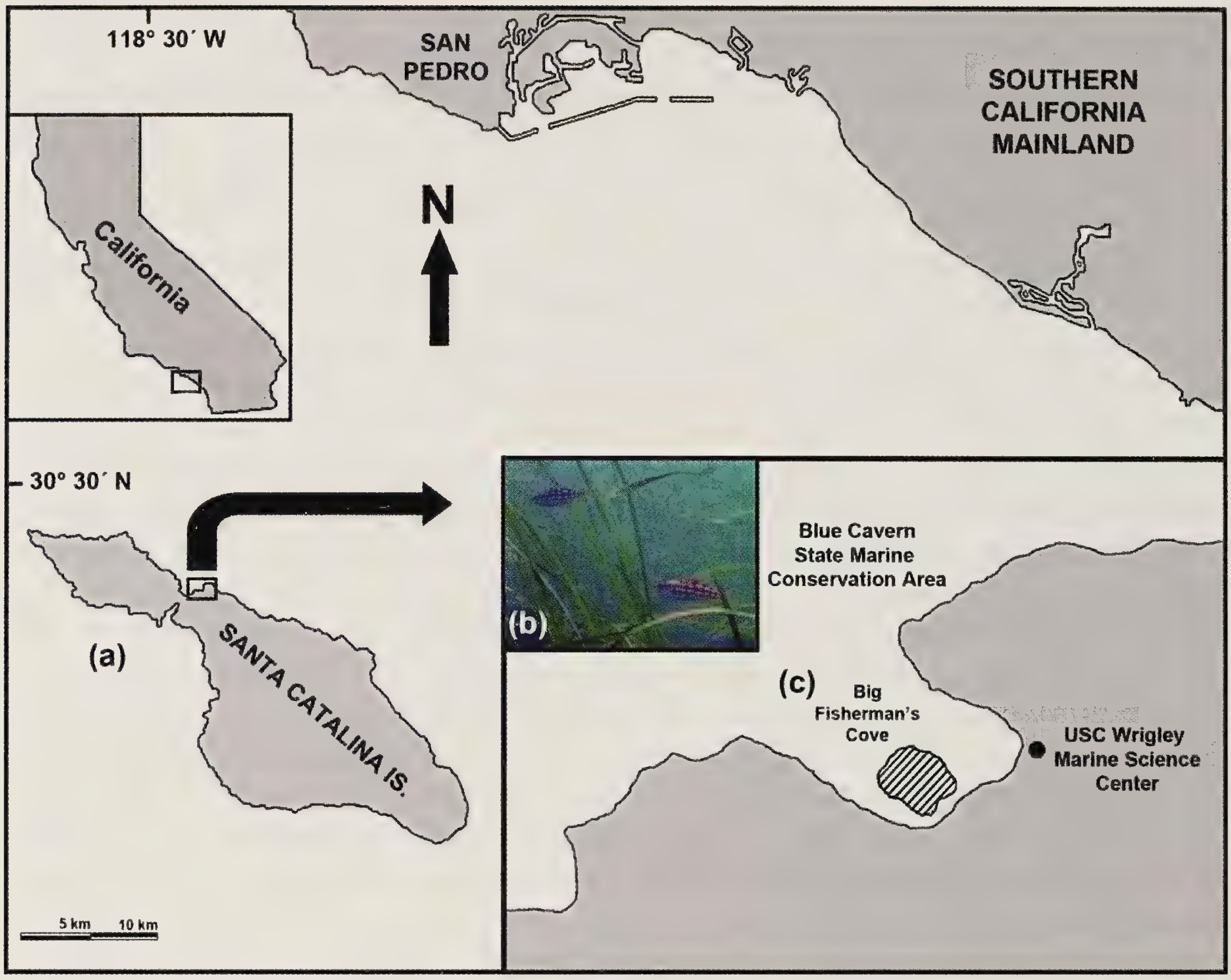

118° 30′ W
SAN PEDRO
SOUTHERN CALIFORNIA MAINLAND
N
California
30° 30′ N
(a)
SANTA CATALINA IS.
5 km
10 km
(b)
Blue Cavern State Marine Conservation Area
(c)
Big Fisherman's Cove
USC Wrigley Marine Science Center

Fig. 1. Map showing the location of (a) Santa Catalina Island relative to the Southern California mainland. Surveys of (b) eelgrass *Z. marina* and kelp bass *P. clathratus* were conducted in (c) Big Fisherman's Cove, which is part of the Blue Cavern State Marine Conservation Area. Hatched area indicates survey site and extent of *Zostera* areal coverage (~0.24 hectares). Map adapted from Froeschke et al. (2006).

covered with macroalgae and kelp that provides a forest habitat for fishes and invertebrates (Abbott and Hollenberg 1992; Parnell et al. 2010). The sandy, inner reaches of the cove (4-12 m depth) support a *Zostera* bed that covers an area ~0.24 ha in size (Obaza and Ginsburg unpublished data). Areal coverage of *Zostera* in Big Fisherman's Cove was estimated using a Trimble® R1 Global Navigational Satellite System (GNSS) receiver held at the water surface in which a scuba diver was tracked while swimming along the perimeter of the bed at depth. Patches of *Zostera* were first documented at this site in 1996 and are likely the result of natural colonization from nearby populations (Engle and Miller 2005).

Fish surveys targeted kelp bass, which are one of the most important recreational species of reef fish off Southern California (Young 1963; Erisman et al. 2011). Typically found in shallow water (3-25 m depth), juveniles feed on benthic invertebrates and switch to a mostly piscivorous diet as adults (Hobson and Chess 1976; Eschmeyer and Herald 1999). Mature individuals form breeding aggregations in the late spring to early fall in which larvae enter the plankton and settle after 28-30 days onto *Zostera* beds (Valle et al. 1999; Allen et al. 2002) and shallow, rocky reefs (Carr 1994; Love et al. 1996; Cordes and Allen 1997; Erisman and Allen 2006). Adult kelp bass exhibit high levels of site fidelity (Mason and Lowe 2010). However, catch and release studies by Carr (1994) and Hartney (1996) indicate that juveniles are unlikely to return to the reef in which they settled (home) after moving to a new location.

Zostera and Kelp Bass Surveys

The structural complexity of *Zostera* habitat, as well as the size and abundance of juvenile kelp bass was measured by scuba divers. Surveys were conducted along four separate, 30-m long benthic transects spaced ~4 m apart. The beginning of each transect was marked with a semi-permanent sand anchor and surveyed along a northwest compass heading of 310 degrees. Structural complexity was defined using three key measurements of *Zostera* habitat: shoot frequency, shoot density and canopy height. Frequency was estimated using a point-intercept approach in which *Zostera* leaf shoots were recorded as either present or absent along each meter interval (from 1 to 30 m) directly beneath the transect line. Density was measured as the total number of leaf shoots counted within four quadrats (0.25 m^2) placed at 10-m intervals (0-30 m) along each transect. Lastly, *Zostera* canopy height was recorded (to the nearest cm) as 80% of the mean length of ≥ 10 haphazardly selected leaf shoots (Short and Durate 2001) within each of the quadrats described above. The product of each of these metrics (i.e., frequency, density and canopy height) was used to create an eelgrass structural index in order to view the collective changes in *Zostera* habitat over time.

Juvenile kelp bass were surveyed visually from 1 m above the benthos and within a 2 m wide swath along each 30 m transect line. Given the importance of *Zostera* habitat to new recruits (Jackson et al. 2001), visual surveys focused on juvenile kelp bass (2.1–10 cm TL; Love et al. 1996) and not adults that may have migrated from other areas. The size and abundance of juveniles was recorded by divers as they swam the length of each transect line. The TL of an individual was recorded to the nearest cm following the methods of Bell et al. (1985). Kelp bass abundance was measured as the total number of juvenile fish recorded on a given transect. Visual estimates of fish length and density are known for a range of different reef fishes and habitats (Sale 1980; Brock 1982; Coyer and Witman 1990; Ebeling and Hixon 1991) and are frequently used to monitor subtidal marine life off Southern California (Pondella et al. 2006; Gillett et al. 2012; Coates et al. 2018).

Kelp Bass Secondary Production

Secondary production was based on visual surveys of length and abundance of juvenile fish using a modified version of the model developed by Claisse et al. (2014). Specifically, secondary production rates were estimated for individual kelp bass observed on a given survey by determining changes in biomass after one month of growth using a weight–length relationship specific to this species. A linear growth function was used, rather than an exponential growth curve, as the former provides a better fit for modeling the growth of young-of-the-year (YOY) fishes (Faunce and Serafy 2008; Yeager et al. 2012; J.T. Claisse pers. comm.).

Fish biomass (i.e., mean wet body weight, W) was calculated from the observed length of kelp bass using the weight-length relationship: $W = a\,TL^{\,b}$, where TL is the total length of individual kelp bass from visual surveys and the constants a and b (0.00813 and 3.03, respectively) are specific growth rates reported for this species (see Froese et al. 2014). The age (months-old) of individual kelp bass was determined using empirical age-at-length values for juveniles (2.1 to 10 cm TL) reported by Love et al. (1996). From these data, a linear growth rate of 1.17 cm TL mo^{-1} was calculated for post-settlement (>2.1 cm TL) kelp bass ≤ 1 year old. Individual kelp bass, whose TL was recorded (to the nearest cm) on dive surveys in Big Fisherman's Cove, were then sorted into one of the following age-at-length bins (AL_1–AL_6): 1 month old, 2.1–3.27 cm TL; 2 months old, 3.28–4.45 cm TL; 3 months old, 4.46–5.63 cm TL; 4 months old, 5.64–6.81 cm TL; 5 months old, 6.82–7.99 cm TL; 6 months old, 8.0–9.17 cm TL). The growth (G) of individual kelp bass from each length bin was calculated using visual survey data as the difference between changes in biomass, estimated by TL, after one month of growth ($\Delta TL = 1.17$ cm mo^{-1}) using the equation: $G = a(TL + \Delta TL)^b - W$.

The instantaneous rate of fish mortality (M) was calculated monthly with the TL of individual kelp bass from each age-at-length bin using the empirical formula reported by Gislason et al. (2010) as follows: $\ln(M) = 0.55 - 1.61 [\ln(TL)] + 1.44 [\ln(L_\infty)] + \ln(k)$, where L_∞ and k (69.8 cm TL and 0.06, respectively) are key life-history parameters specific to kelp bass reported by Love et al. (1996). We selected this approach because it is the best-supported estimator for determining the number of individuals that survive to successive life stages (Lv and Pitchford 2007; Claisse et al. 2014). Fish mortality rates were estimated on a monthly basis (as opposed to an annual schedule). Survivorship (S) of kelp bass was then calculated using the monthly length- and species-specific exponential rate of fish mortality for each month sampled using the equation: $S = e^{-M}$.

Accumulated biomass (i.e. somatic production, P_s) of kelp bass was calculated on a monthly basis as the product of fish growth (G), survivorship (S) within a given age-at-length bin and fish density (N; number of juvenile kelp bass recorded within a 2 m wide swath along each of the four, 30 m transects [= 240 m^2 total survey area]) using the equation: $P_s = (G)(S)(N)$. Total secondary production (P_T) was calculated as the monthly sum (Σ_m) of recruitment (P_R, accounts for YOY fish growth) and somatic production (P_S) for each of the six post-settlement age-at-length bins (AL_1-AL_6) recorded over the course of the study as follows: $P_T = \Sigma_m (P_R + P_{AL1} + P_{AL2} + P_{AL3} + P_{AL4} + P_{AL5} + P_{AL6})$.

Data Analysis

The relationship between the structural complexity of *Zostera* habitat and the abundance of juvenile kelp bass was analyzed using a multiple regression model. Visual estimates of fish density were tested for heteroscedasticity and treated as individual, monthly events. Interactions among the different predictor variables of *Zostera* habitat (leaf shoot frequency, density and canopy height), measured across different months, were presumed to have at least one common variable between them. Temporal autocorrelation among covariate months and years was accounted for by applying a generalized least squares (GLS) and maximum likelihood (ML) estimation procedure to all statistical models tested. Akaike's Information Criterion (AIC) was used to determine the model of best fit. Comparisons between the different predictor variables were tested for multicollinearity using a Farrar chi-square test. Although the relationship between *Zostera* shoot frequency and canopy height was collinear ($\chi^2 = 2.39$, $p < 0.05$), the relationship between each of these factors in addition to shoot density was not strong enough to warrant a statistical correction. Furthermore, variance inflation factors for each of the *Zostera* predictor variables were not statistically significant (critical value < 2). Therefore, multicollinearity was unlikely to pose an issue (Graham 2003) for estimating the relationship between the structural complexity of *Zostera* and the presence of kelp bass.

Comparisons between the abundance of kelp bass and each of the predictor variables of *Zostera* habitat structure were analyzed separately using a GLS approach, and subsequently evaluated by AIC using the information-theoretic approach for analyzing

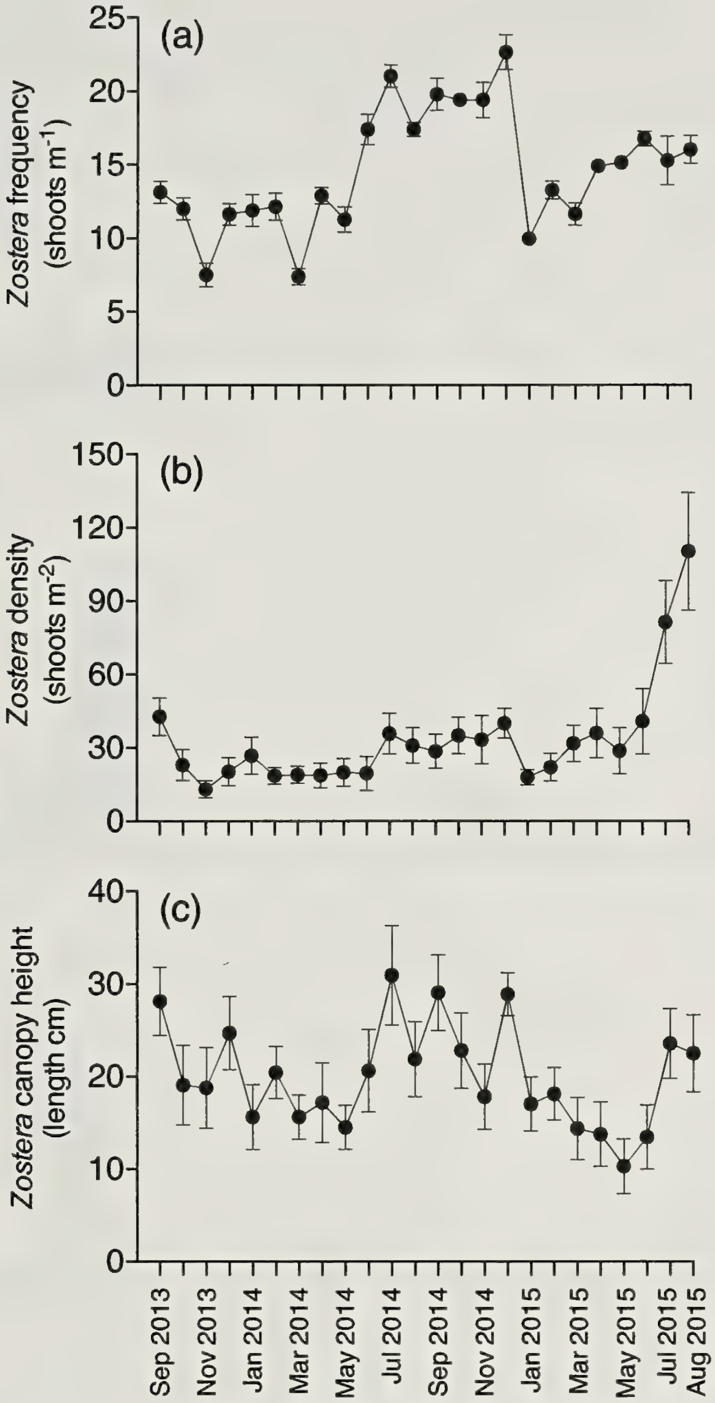


Fig. 2. Monthly changes in (a) frequency, (b) density and (c) canopy height of eelgrass *Zostera marina* recorded from September 2013 to August 2015 in Big Fisherman's Cove. Values are means ± 1 SE. Where not shown, errors fell into the graphical representation of the data point.

ecological data developed by Burnham and Anderson (2002). Given the relatively low sample sizes, a second-order (i.e., corrected) information criterion (AICc) approach was used in place of the general AIC estimator. These values were, in turn, compared to kelp bass abundance and secondary production using a GLS approach. Error values reported are ± 1 SE of the mean. All data were analyzed using R Statistical Software (R Core Team 2015) with the *dplyr* (Wickham et al. 2015) and *nlme* (Pinheiro et al. 2015) packages.

Results

The frequency of *Zostera* leaf shoots (Fig. 2a) increased nearly 3-fold from March to July 2014 (average = 7.4 ± 0.6 to 21.0 ± 0.78 shoots m^{-1}, respectively; ANOVA, $F_{1,9} = 8.13, p < 0.05$) and remained relatively unchanged until December 2014 (average = ANOVA, $F_{1,11} = 26.9, p = 0.0004$). Shoot frequency then dropped 32% from an average of

Table 1. Factor type (ψ), AICc scores, AICc differences (Δ) and Akaike weights (ω) for predicting the use of *Zostera* habitat structure by juvenile kelp bass *Paralabrax clathratus*. The model with the smallest ΔAICc value was selected as the best fit: ℓ are the maximized log likelihoods, Cumul (ω) are the cumulative Akaike weights and Coeff (ψ) are the factor coefficients.

ψ	AICc	ΔAICc	ω	ℓ	Cumul (ω)	Coeff (ψ)
Canopy height	257.48	0	0.37	-122.08	0.37	1.56
Shoot density						0.84
Canopy height	258.55	1.06	0.21	-124.22	0.59	1.81
Canopy height	259.45	1.97	0.14	-123.06	0.73	1.43
Shoot frequency						0.97
Canopy height	259.85	2.37	0.11	-121.46	0.84	1.33
Shoot density						0.72
Shoot frequency						0.69
Shoot density	260.96	3.47	0.07	-123.81	0.90	0.87
Shoot frequency						1.52
Shoot density	261.31	3.83	0.05	-123.60	0.96	0.32
Shoot frequency	261.90	4.42	0.04	-125.90	1.00	1.81

19.9 ± 0.4 shoots m^{-1} between July and December 2014 to 13.6 ± 0.33 shoots m^{-1} between January and August 2015 (ANOVA, $F_{1,13} = 26.1$, $p = 0.0003$). Alternatively, the density of *Zostera* leaf shoots (Fig. 2b) increased 39% from an average of 22.2 ± 2.54 shoots m^{-2} between September 2013 and June 2014 to 30.9 ± 1.93 shoots m^{-2} between July 2014 to May 2015 (ANOVA, $F_{1,20} = 7.7$, $p < 0.05$). From here, shoot density more than tripled in December 2015, reaching a peak value of 110.3 ± 24.1 shoots m^{-2} (ANOVA, $F_{1,13} = 21.5$, $p = 0.0006$). Finally, despite month-to-month fluctuations in the canopy height of *Zostera* (Fig. 2c), the overall length of leaf shoots did not significantly change throughout the study period (average $= 20.0 \pm 1.13$ cm; ANOVA, $F_{1,23} = 0.33$, $p = 0.57$).

A total of 1,419 kelp bass were recorded within the *Zostera* study site in Big Fisherman's Cove (Fig. 3). Nearly 87% of fish were identified as juveniles (2.1 to 10 cm TL; Love et al. 1996) with 84% of individual kelp bass estimated as younger than 6 months of age (<9.18 cm TL). Kelp bass were not observed in the *Zostera* study area on the following dates: February 2014, April 2014, January 2015 and May 2015. The number of kelp bass recorded for each age-at-length bin ranged from 124 to 311 individuals (average $= 202.7 \pm 26.8$ kelp bass) over the course of the study (Fig. 3a-g). Kelp bass abundance across all age-length bins varied seasonally with the greatest number of fish recorded in the summer and fall months (June to November) and the fewest during the winter and spring (December to May) averaging 98.3 ± 14.9 and 19.9 ± 9.3 kelp bass mo^{-1}, respectively (ANOVA, $F_{1,23} = 19.9$, $p = 0.0002$).

Seasonal changes in *Zostera* habitat structure (Fig. 4a) were observed throughout the study period reaching its peak in the summer and fall (June to November, average $= 15{,}519 \pm 3{,}099$) and dropping to its lowest point in the winter and spring (December to May, $6{,}381 \pm 1{,}838$; ANOVA, $F_{1,23} = 6.34$, $p < 0.05$). Likewise, seasonal changes in *Zostera* habitat structure were significantly correlated with juvenile kelp bass abundance ($\beta_{GLM} = 0.015$, $p < 0.001$; Fig. 4a). Results of the AICc goodness-of-fit model selection are shown in Table 1. The model that best approximated the use of *Zostera* habitat structure by kelp bass, as indicated by the smallest ΔAICc score, included eelgrass shoot density and canopy height as the predictor variables (AICc = 257.5). Two other models accepted by the AIC$_c$ statistic (ΔAICc < 2) also included *Zostera* canopy height as a predictor

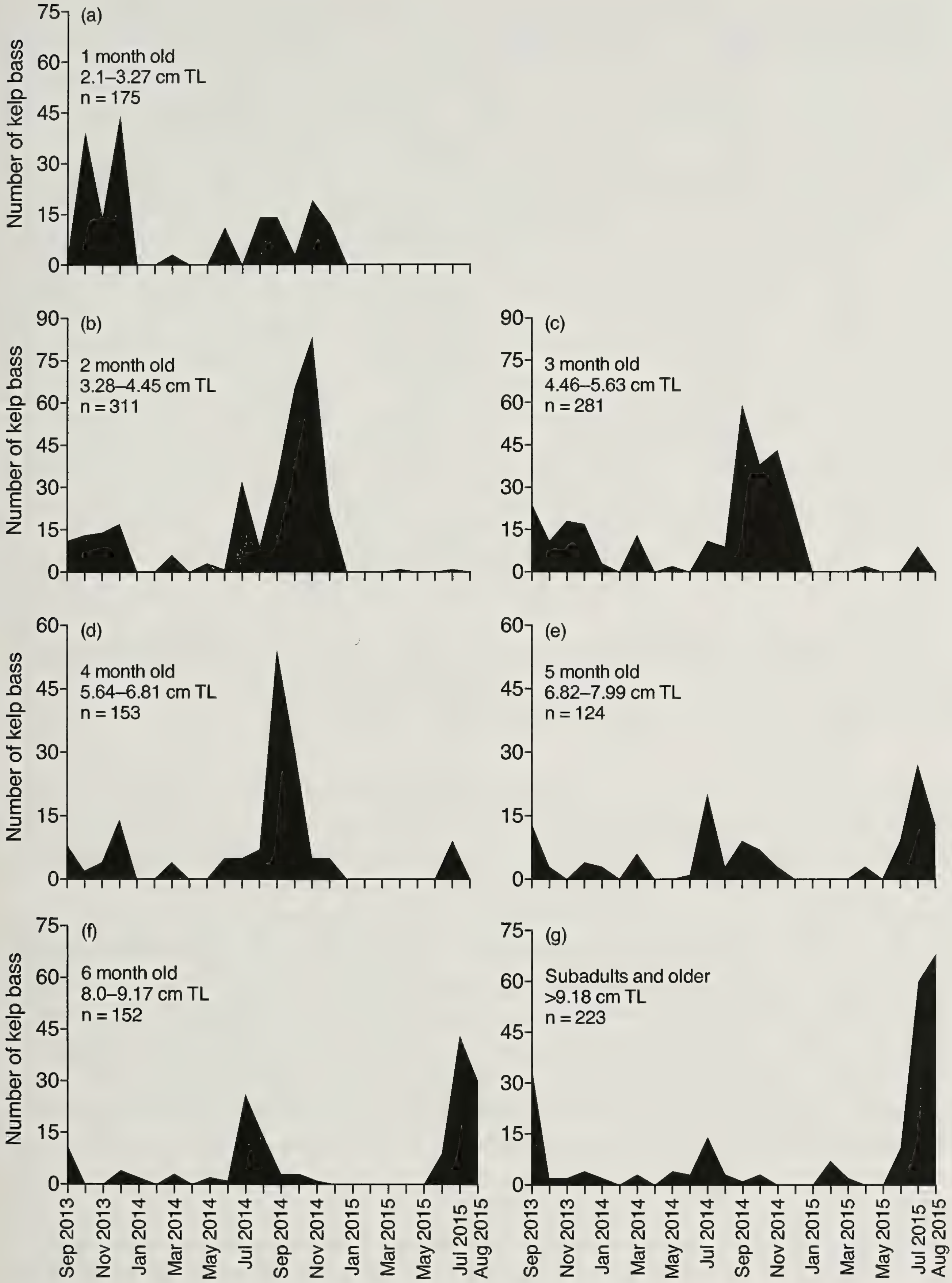


Fig. 3. Monthly abundance of kelp bass *P. clathratus* observed amongst eelgrass *Z. marina* habitat in Big Fisherman's Cove. A total of 1,419 kelp bass were recorded from September 2013 to August 2015. Kelp bass observed during visual surveys were sorted into different age-at-length bins as follows: (a) 1 month old, 2.1–3.27 cm TL, (b) 2 month old, 3.28–4.45 cm TL, (c) 3 month old, 4.46–5.63 cm TL, (d) 4 month old, 5.64–6.81 cm TL, (e) 5 month old, 6.82–7.99 cm TL, (f) 6 month old, 8.0–9.17 cm TL and (g) > 9.18 cm (subadult stage and older). On February and April 2014 and January and May 2015, no kelp bass were observed in the *Zostera* study area.

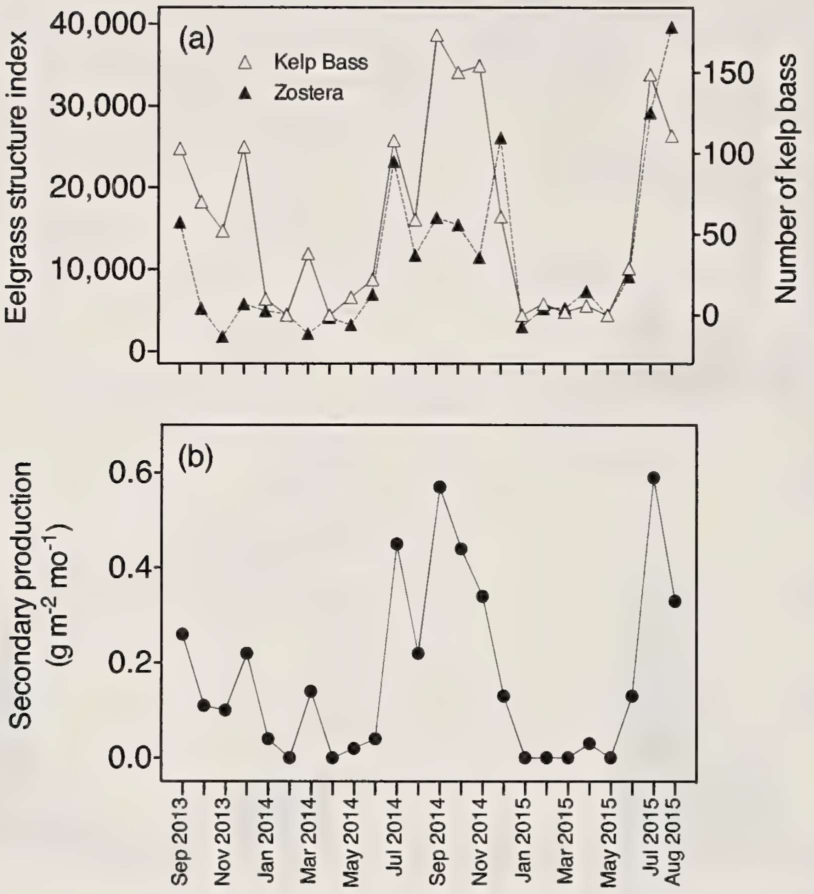


Fig. 4. Relationship between the (a) structural complexity of eelgrass *Z. marina* habitat and kelp bass *P. clathratus* abundance, and (b) rates of secondary production in juvenile kelp bass surveyed monthly from September 2013 to August 2015 in Big Fisherman's Cove. Eelgrass structure index defined as the product of the mean leaf shoot frequency, density and canopy height of *Zostera*.

variable: both on its own (AICc = 258.6) and when combined with leaf shoot frequency (AICc = 259.5). ΔAICc scores for the remaining candidate models exceeded the threshold value for the best-fit model (ΔAICc < 2) and, therefore, were not considered an accurate predictor of the relationship between kelp bass and *Zostera* habitat structure.

Rates of secondary production calculated for juvenile kelp bass (range = 0.1 to 0.59 $g\ m^{-2}\ mo^{-1}$) in Big Fisherman's Cove were significantly correlated with monthly changes in *Zostera* habitat structure throughout the study ($\beta_{GLM} = 0.21$, $p = 0.0005$; Fig. 4, Table 2). Secondary production in kelp bass was 6-times higher in the summer and fall months (June to November, average = 0.3 ± 0.05 $g\ m^{-2}\ mo^{-1}$) than in the winter and spring (December to May, average = 0.05 ± 0.02 $g\ m^{-2}\ mo^{-1}$). However, interannual shifts in fish secondary production from 2013 to 2015 were not observed (range = 1.62 ± 0.92 to 2.39 ± 0.70 $g\ m^{-2}\ yr^{-1}$; $\beta_{GLM} = 0.56$, $p = 0.07$; Table 2).

Discussion

Data presented here provide an important baseline of fish biomass and recruitment associated with *Zostera* habitat in the absence of significant anthropogenic impacts, and will help to define the role of seagrass within the larger context of nearshore coastal ecosystems. Because juvenile fishes are known to seek refuge in areas with structured habitat such as seagrass (Hovel et al. 2002; Pihl et al. 2006), the positive relationship between the abundance of kelp bass and different metrics (shoot frequency, shoot density and canopy height; Fig. 2) used to evaluate *Zostera* structure was expected. In California, eelgrass mitigation policies established by NOAA Fisheries require that measurements of leaf shoot density and areal coverage (frequency, in this study) are used as a proxy for estimating

Table 2. Monthly estimates of total length (TL) and secondary production recorded for juvenile kelp bass *P. clathratus* in Big Fisherman's Cove. TL values are means ± SE. Zero TL values indicate survey dates in which individual kelp bass were either absent from the *Zostera* study area or >9.17 cm TL (subadult stage and older).

Survey date	TL (cm)	Secondary production ($g\ m^{-2}\ mo^{-1}$)
Sept 2013	7.78 ± 0.39	0.26
Oct 2013	4.89 ± 0.68	0.11
Nov 2013	3.97 ± 0.24	0.1
Dec 2013	4.54 ± 0.15	0.22
Jan 2014	6.28 ± 2.40	0.04
Feb 2014	0	0
Mar 2014	5.80 ± 0.37	0.14
Apr 2014	0	0
May 2014	12.0 ± 0.33	0.02
June 2014	8.73 ± 0.21	0.04
July 2014	7.27 ± 0.53	0.45
Aug 2014	5.87 ± 0.45	0.22
Sept 2014	5.04 ± 0.09	0.57
Oct 2014	5.10 ± 0.15	0.44
Nov 2014	4.36 ± 0.07	0.34
Dec 2014	4.32 ± 0.12	0.13
Jan 2015	0	0
Feb 2015	15.2 ± 0.20	0
Mar 2015	7.50 ± 0.01	0
Apr 2015	4.33 ± 0.48	0.03
May 2015	0	0
June 2015	9.39 ± 0.43	0.13
July 2015	9.12 ± 0.25	0.59
Aug 2015	9.12 ± 0.12	0.33

the function of eelgrass habitat. However, a significant finding from the current study is that the canopy height of leaf shoots, by itself, is a better predictor of the use of *Zostera* habitat by kelp bass (Table 1). Similar sets of measurements on the spatial patterns and variability of seagrass-fish assemblages report that canopy height is a key determinant of juvenile fish density (Gullström et al. 2008), and leaf shoot density, on its own, is a poor indicator of the abundance of fishes and decapods associated with a given eelgrass bed (Worthington et al. 1992). In addition to providing essential habitat and protection to fishery species, seagrasses provide a variety of ecosystem services whose economic value, in terms of the abundance and density of seagrass beds as a whole, far outweigh their ecological function (Barbier et al. 2011; Schubert et al. 2015). Survey metrics that capture the three-dimensional complexity of *Zostera* habitat will help to better understand the ecological functions of these communities.

Higher rates of secondary production in juvenile kelp bass coincided with increases in *Zostera* habitat structure (Fig. 4), as does the spawning season for this fish species, which reaches its peak during the summer months from June to August (Love et al. 1996; Cordes and Allen 1997; Erisman and Allen 2006). These findings highlight the need for time series data with seasonal patterns across multiple years to provide a more accurate estimate of variability. A reduction in the sampling frequency of fish at a given location, as dictated by limited access or resource availability, could yield dramatically different estimates of secondary production on an annual scale. For example, if monthly rates of secondary production for juvenile kelp bass (Table 2) were calculated on a quarterly basis, rates would be either over- or underestimated by as much as 8 to 27%, respectively (quarterly schedule begins on either September or November 2013; average = 2.24 ± 0.97 and 1.52 ± 0.96 g m^{-2} yr^{-1}, respectively; compare to 24-month average = 2.08 ± 0.46 g m^{-2} yr^{-1}). Future studies should utilize both existing patterns of habitat use and spatial variability as a best estimate of the abundance and distribution of animals in a given location. In the case that fish movement patterns are limited to a specific area (cf. blue rockfish *Sebastes mystinus*: Jorgensen et al. 2006), a single sampling event on an annual basis may be sufficient.

Annual rates of secondary production calculated for juvenile kelp bass in this study approximate those reported for adult fishes in seagrass habitat (0.24 to 7.08 g m^{-2} yr^{-1}, Table 2; compare to 3.8 to 14.6 g m^{-2} yr^{-1}: Adams 1976; Edgar and Shaw, 1995; Jeong et al. 2009). Given the increased protection of kelp bass off Catalina Island through enhanced conservation and management plans (essential fish habitat and marine protected areas), coupled with their relatively small home range ($<$ 0.33 ha, Lowe et al. 2003), enhanced settlement and recruitment within coastal *Zostera* beds are likely to play an important role in the export of adult fish to adjacent areas (Domeier 2004; Watson et al. 2010). Claisse et al. (2014) report markedly higher rates of annual secondary production amongst fishes on offshore oil platforms (range = 104.7 to 886.8 g m^{-2} yr^{-1}) in the same region as this study. Although both habitats may perform a nursery function (Love et al. 2006), the complex, hardscape structure of the offshore oil platform itself is distributed throughout the water column and is therefore better suited for intercepting larvae. *Zostera* beds, on the other hand, while associated with low-relief ($<$1 m above the benthos) nearshore habitats, are an important nursery ground and refuge for a variety of animals and may undergo high rates of species turnover for both reef fishes and invertebrates (Seitz and Ewers Lewis 2018). Nonetheless, research findings presented here indicate that *Zostera* is an important contributor to secondary production in kelp bass, which is one of the most important nearshore recreational species off the Southern California coast (Love et al. 1996; Erisman and Allen 2006; Horning 2009).

A common goal of resource monitoring is the development of biological indicators that provide rapid assessment of ecosystem function. Fish are useful as bioindicators because they are relatively easy to see, can disperse from stressed habitats and are economically important (Whitfield and Elliot 2002). The resources required to monitor secondary production at a level appropriate to detect significant impacts is daunting, but may be comparable, or perhaps less intensive, than other bioindicators (cf. carbon-to-nitrogen ratios, rhizome sugars and above-ground biomass; McMahon et al. 2013) used to assess the quality of *Zostera* habitats and how they might change over time. Further research is required to assess changes in secondary production in response to different impact types such as, sediment disturbance and invasive species encroachment. Kelp bass make for an effective case study of ecosystem function and services because these fish are common throughout the Southern California Bight and are an important component of biomass and recruitment associated with seasonal changes in *Zostera* habitat structure. Results from this study provide a baseline for the use of fish secondary production as an indicator of the health of eelgrass ecosystems.

The seasonal use of coastal *Zostera* habitat as a nursery ground by juvenile kelp bass off Catalina Island during the summer and fall months coupled with the presence of significantly fewer fish in the winter and spring (Fig. 3 and 4) suggests that a substantial amount of biomass could be exported to nearby coastal habitats. These findings support previous work on the export of energy and nutrients across coastal habitat boundaries through the transfer of fish biomass (Deegan 1993). We postulate this on the assumption that juvenile kelp bass vacate eelgrass beds after reaching a certain ontogenetic stage, but further work is needed to verify the movement of kelp bass throughout their life cycle. While the relationship among juvenile habitats is well defined in tropical areas (Nagelkerken et al. 2000), far less is known in temperate regions such as the Pacific Coast. This study is one of the first in the region to provide quantitative data that support a possible ontogenetic shift in juvenile fish from coastal *Zostera* beds to adjacent habitats. Future studies on the export of fish biomass from seagrass beds (Gillanders 2006) will allow conservation and management efforts to focus on key marine resources such as protected areas around the California Channel Islands, which provide a major contribution to adult populations of ecologically and economically valuable species. Likewise, quantitative assessments of habitat function are beneficial for resource managers to determine the mitigation costs (e.g., habitat equivalency analysis) associated with a loss in natural resource services (Dunford et al. 2004). Further investigations of fish secondary production in nearshore coastal ecosystems are required to provide new insights into the mechanisms that contribute to the growth, dispersal and connectivity among populations and will help to communicate the significance of marine resource conservation with both the general public and stakeholder groups.

Acknowledgements

We thank the following USC Dornsife Environmental Studies Program alumni: Wendy Beylik, Michele Felberg, Madison Guest, Audrey Looby, Tyler Schiffman, Kali Staniec, Christine Sur, Laura Wang and Sarah Wood for their assistance collecting field data at the USC Wrigley Marine Science Center. Eric Chavez and Bryant Chesney from NOAA Fisheries also provided valuable assistance during the study. Reviews of the manuscript by Scott Applebaum, Jeremy Claisse, Jonathan Williams and two anonymous reviewers greatly improved the document.

Literature Cited

Abbott, I.A., and G.J. Hollenberg. 1992. Marine algae of California. Stanford University Press, CA. 844 pp.

Adams, S.M. 1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II. Functional analysis. J. Exp. Biol. Ecol., 22:293–311.

Allen, L.G., A.M. Findlay, and C.M. Phalen. Structure and standing stock of the fish assemblages of San Diego Bay, California from 1994 to 1999. BSCAS, 101:49–85.

Altstatt, J., R. Ambrose, J. Carroll, J. Coyer, J. Wible, and J. Engle. 2014. Eelgrass meadows return to Frenchy's Cove, Anacapa Island: recovery ten years after successful transplantation. West. North. Am. Nat. 7:500–517.

Barbier, E.B., S.D. Hacker, C. Kennedy, E.W. Koch, A.C. Stier, and B.R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr., 81:169–193.

Bas Ventín, L.B., J. de Souza Troncoso, and S. Villasante. 2015. Towards adaptive management of the natural capital: disentangling trade-offs among marine activities and seagrass meadows. Mar. Pollut. Bull., 101:29–38.

Bell, J.D., G.J.S. Craik, D.A. Pollard, and B.C. Russell. 1985. Estimating length frequency distributions of large reef fish underwater. Coral Reefs, 4:41–44.

Brock, R.E. 1982. A critique of a visual census method for assessing coral reef fish populations. Bull. Mar. Sci., 32:269–276.

Burkholder, J.M., D.A. Tomasko, and B.W. Touchette. 2007. Seagrasses and eutrophication. J. Exp. Biol. Ecol., 350:46–72.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York. 488 pp.

Carr, M.H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology, 75: 1320–1333.

Claisse, J.T., D.J. Pondella II, M.S. Love, L.A. Zahn, C.M. Williams, J.P. Williams, and A.S. Bull. 2014. Oil platforms off California are among the most productive marine fish habitats globally. PNAS, 111:15462–15467.

Coates, J.H., K. Schiff, R.D. Mazor, D.J. Pondella, R. Schaffner, and E. Whiteman, 2018. Development of a biological condition assessment index for shallow, subtidal rocky reefs in Southern California, USA. Mar. Ecol., 39:e12471.

Coles, R., F. Short, M. Fortes, and J. Kuo. 2014. Twenty years of seagrass networking and advancing seagrass science: the international seagrass biology workshop series. Pac. Conserv. Biol., 20:8–16.

Cordes, J.F., and L.G. Allen. 1997. Estimates of age, growth, and settlement from otoliths of young-of-the-year kelp bass (*Paralabrax clathratus*). BSCAS, 96:43–60.

Coyer J, and J. Witman. 1990. The underwater catalog: A guide to methods in underwater research. Shoals Marine Laboratory, Cornell University, New York. 72 pp.

Davis, G.E. 2005. Science and society: marine reserve design for the California Channel Islands. Conserv. Biol., 19:1745–1751.

Dawson, E.Y., and M.S. Foster. 1982. Seashore plants of California. Volume 47, University of California Press. 226 pp.

Deegan, L.A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Can. J. Fish. Aquat. Sci., 50:74–79.

DeMartini, E.E., A.M. Barnett, T.D. Johnson, and R.F. Ambrose. 1994. Growth and production estimates for biomass-dominant fishes on a Southern California artificial reef. Bull. Mar. Sci., 55:484–500.

Domeier, M.L. 2004. A potential larval recruitment pathway originating from a Florida marine protected area. Fish. Oceanogr., 13:287–294.

Dunford, R.W., T.C. Ginn, and W.H. Desvousges. 2004. The use of habitat equivalency analysis in natural resource damage assessments. Ecol. Econ. 48:49–70.

Ebeling A.W., and M.A. Hixon. 1991. Tropical and temperate reef fishes: comparison of community structures. Pp 509–563 in The Ecology of Fishes on Coral Reefs. (P.F. Sale, ed.). Academic Press, San Diego.

Edgar, G.J., and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. J. Exp. Biol. Ecol., 194:53–81.

Engle, J.M., and K.A. Miller. 2005. Distribution and morphology of eelgrass (*Zostera marina* L.) at the California Channel Islands. Pp. 405–414 in The Proceedings of the Sixth California Islands Symposium. (D.K. Garcelon and C.A. Schween, eds.) National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, CA. 508 pp.

Erisman, B.E., and L.G. Allen. 2006. Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard) from Santa Catalina Island, California, USA. J. Fish Biol., 68:157–184.

———, Allen L.G., J.T. Claisse, D.J. Pondella, E.F. Miller, and J.H. Murray. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can. J. Fish. Aquat. Sci., 68:1705–1716.

Eschmeyer, W.N., and E.S. Herald. 1999. A field guide to Pacific coast fishes: North America. Houghton Mifflin Harcourt. 352 pp.

Faunce, C.H., and J.E. Serafy. 2008. Growth and secondary production of an eventual reef fish during mangrove residency. Estuar. Coast. Shelf. Sci., 79:93–100.

Findlay, A.M., and L.G. Allen. 2002. Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus*. Mar. Ecol. Prog. Ser., 238:237–248.

Froeschke, J.T., L.G. Allen, and D.J. Pondella. 2006. The fish assemblages inside and outside of a temperate marine reserve in Southern California. BSCAS, 105:128–142.

Froese, R., J.T. Thorson, and R.B. Reyes. 2014. A Bayesian approach for estimating length-weight relationships in fishes. J. Appl. Ichthyol., 30:78–85.

Gillanders, B.M., K.W. Able, J.A. Brown, D.B. Eggleston, and P.F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser., 247:281–295.

———. 2006. Seagrasses, Fish and Fisheries. Pp. 500–536 in Seagrasses: Biology, Ecology and Conservation. (A.W.D. Larkum, R.J. Orth, and C.M. Duarte, eds.) Springer, The Netherlands. 691 pp.

Gillett, D.J., D.J. Pondella, J. Freiwald, K.C. Schiff, J.E. Caselle, C. Shuman, and S.B. Weisberg. 2012. Comparing volunteer and professionally collected monitoring data from the rocky subtidal reefs of Southern California, USA. Environ. Monit. Assess. 184:3239–3257.

Gislason, H., N. Daan, J.C. Rice, and J.G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish Fish., 11:149–158.

Gullström, M., M. Bodin, P.G. Nilsson, and M.C. Öhman. 2008. Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Mar. Ecol. Prog. Ser., 363:241–255.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84: 2809–2815.

Hartney, K.B. 1996. Site fidelity and homing behaviour of some kelp-bed fishes. J. Fish Biol., 49:1062–1069.

Heck, K.L. Jr., G. Hays, and R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser., 253:123–136.

Hobson, E.S., and J.R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., 74:567–598.

Hoffman, R.S. 1986. Fishery utilization of eelgrass (*Zostera marina*) beds and non-vegetated shallow water areas in San Diego Bay. Southwest Region, NOAA, National Marine Fisheries Service. 29 pp.

Horning, O. 2009. Kelp bass. CalCOFI, 50:30–32.

Hovel, K.A., M.S. Fonseca, D. Myer, W. Kenworthy, and P. Whitfield. 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Mar. Ecol. Prog. Ser., 243:11–24.

Jackson, E.L., A.A. Rowden, M.J. Attrill, S.J. Bossey, and M.B. Jones. 2001. The importance of seagrass beds as a habitat for fishery species. Oceanogr. Mar. Biol., 39:269–304.

Jeong, S.J., O.H. Yu, and H.-L. Suh. 2009. Reproductive patterns and secondary production of *Gammaropsis japonicus* (Crustacea, Amphipoda) on the seagrass Zostera marina of Korea. Hydrobiologia, 623:63–76.

Johnson, T.D., A.M. Barnett, E.E. DeMartini, L.L. Craft, R.F. Ambrose, and L.J. Purcell. 1994. Fish production and habitat utilization on a Southern California artificial reef. Bull. Mar. Sci., 55: 709–723.

Jorgensen, S.J., D.M. Kaplan, A.P. Klimley, S.G. Morgan, M.R. O'Farrell, and L.W. Botsford. 2006. Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. Mar. Ecol. Prog. Ser., 327:157–170.

Kamimura, Y., A. Kasai, and J. Shoji. 2011. Production and prey source of juvenile black rockfish *Sebastes cheni* in a seagrass and macroalgal bed in the Seto Inland Sea, Japan: estimation of the economic value of a nursery. Aquat. Ecol., 45:367–376.

Long, W.J.L., and R.M. Thom. 2001. Improving seagrass habitat quality. Pp. 407–423 in Global Seagrass Research Methods. (F.T. Short and, R.G. Coles, eds.) Elsevier, Amsterdam. 482 pp.

Love, M.S., A. Brooks, D. Busatto, J. Stephens, and P.A. Gregory. 1996. Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer* from the Southern California bight. Fish. Bull., 94:472–481.

———, D.M. Schroeder, W. Lenarz, A. MacCall, A.S. Bull, and T. Lyman. 2006. Potential use of offshore marine structures in rebuilding an overfished rockfish species, bocaccio (*Sebastes paucispinis*). Fish. Bull., 104:383–390.

Lowe, C.G., D.T. Topping, D.P. Cartamil, and Y.P. Papastamatiou. 2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. Mar. Ecol. Prog. Ser., 256:205–216.

Lv, Q., and J.W. Pitchford. 2007. Stochastic von Bertalanffy models, with applications to fish recruitment. J. Theor. Biol., 244:640–655.

Mason, T.J., and C.G. Lowe. 2010. Home range, habitat use, and site fidelity of barred sand bass within a Southern California marine protected area. Fish. Res., 106, 93–101.

McMahon, K., C. Collier, and P.S. Lavery. 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecol. Indic., 30:7–15.

Mendoza-Carranza, M., and J.A. Rosales-Casian. 2002 Feeding ecology of juvenile kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) in Punta Banda Estuary, Baja California, Mexico. BSCAS, 101:103–117.

Nagelkerken, I., G. van der Velde, M.W. Gorissen, G.J. Meijer, T. van't Hof, and C. den Hartog. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes using a visual census technique. Estuar. Coast. Shelf. Sci., 51:31-44.

Obaza, A., R. Hoffman, and R. Clausing. 2015. Long-term stability of eelgrass fish assemblages in two highly developed coastal estuaries. Fisheries. Manag. Ecol., 22:224–238.

Parnell, P.E., P.K. Dayton, R.A. Fisher, C.C. Loarie, and R.D. Darrow. 2010. Spatial patterns of fishing effort off San Diego: implications for zonal management and ecosystem function. Ecol. Appl., 20:2203–2222.

Parsons, D.M., C. Middleton, K.T. Spong, G. Mackay, M.D. Smith, and D. Buckthought. 2015. Mechanisms explaining nursery habitat association: how do juvenile snapper (*Chrysophrys auratus*) benefit from their nursery habitat? PLoS One, 10:1–15.

Pihl, L., S. Baden, N. Kautsky, P. Rönnbäck, T. Söderqvist, M. Troell, and H. Wennhage. 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuar. Coast. Shelf. Sci., 67:123–132.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2015. nlme: Linear and nonlinear mixed effects models, R package version 3.1–126.

Pondella, D.J., L.G. Allen, M.T. Craig, and B. Gintert. 2006. Evaluation of eelgrass mitigation and fishery enhancement structures in San Diego Bay, California. Bull. Mar. Sci., 78:115–131.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Risgaard-Petersen, N., T. Dalsgaard, S. Rysgaard, P.B. Christensen, J. Borum, K. McGlathery, and L.P. Nielsen. 1998. Nitrogen balance of a temperate eelgrass *Zostera marina* bed. Mar. Ecol. Prog. Ser., 174:281–291.

Saarman, E.T., and M.H. Carr. 2013. The California Marine Life Protection Act: A balance of top down and bottom up governance in MPA planning. Mar. Policy, 41:41–49.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol., 18:367–421.

Schubert, P.R., W. Hukriede, R. Karez, and T.B.H. Reusch. 2015. Mapping and modeling eelgrass *Zostera marina* distribution in the western Baltic Sea. Mar. Ecol. Prog. Ser., 522:79–95.

Schultz, S.T., C. Kruschel, T. Bakran-Petricioli, and D. Petricioli. 2015. Error, power, and blind sentinels: the statistics of seagrass monitoring. PLoS One, 10:1–32.

Seitz, R.D., and C.J. Ewers Lewis. 2018. Loss of seagrass results in changes to benthic infaunal community structure and decreased secondary production. Bull. Mar. Sci., 94:1273–1292.

Shelton, A.O., T.B. Francis, B.E. Feist, G.D. Williams, A. Lindquist, and P.S. Levin. 2017. Forty years of seagrass population stability and resilience in an urbanizing estuary. J. Ecol., 105:458–470.

Short, F.T., and C.M. Duarte. 2001. Methods for the measurement of seagrass growth and production. Pp. 155–198 in Global Seagrass Research Methods. (F.T. Short and, R.G. Coles, eds.) Elsevier, Amsterdam. 482 pp.

Valle, C.F., J.W. O'Brien, and K.B. Wiese. 1999. Differential habitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California. Fish. Bull., 97:646–660.

Warren, M.A., R.S. Gregory, B.J. Laurel, and P.V.R. Snelgrove. 2010. Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. J. Exp. Biol. Ecol., 394:154–160.

Watson, J.R., S. Mitarai, D.A. Siegel, J.E. Caselle, C. Dong, and J.C. McWilliams. 2010. Realized and potential larval connectivity in the Southern California bight. Mar. Ecol. Prog. Ser., 401:31–48.

Whitfield, A.K., and M. Elliott. 2002. Fishes as indicators of environmental and ecological changes within estuaries; a review of progress and some suggestions for the future. J. Fish Biol., 61:229–250.

Wickham, H., R. Francois, L. Henry, and K. Müller. 2015. dplyr: A grammar of data manipulation, R package version 0.4.3.

Williams, C.M., J.P Williams, J.T. Claisse, D.J. Pondella, M.L. Domeier, and L.A. Zahn. 2013. Morphometric relationships of marine fishes common to central California and the Southern California Bight. BSCAS, 112:217–227.

Worthington, D.G., D.J. Ferrell, S.E. McNeill, and J.D. Bell. 1992. Effects of the shoot density of seagrass on fish and decapods: are correlations evident over larger spatial scales? Mar. Biol., 112:139–146.

Yeager, L.A., C.L. Acevedo, and C.A. Layman. 2012. Effects of seascape context on condition, abundance, and secondary production of a coral reef fish, *Haemulon plumierii*. Mar. Ecol. Prog. Ser., 462: 231–240.

Young, P.H. 1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947–1958. Fish. Bull., 122:1–67.

Bull. Southern California Acad. Sci.
118(3), 2019, pp. 173–199

Temporal and Volumetric Characteristics of Lagoons in the Santa Monica Bay and the Passage Implications for Southern Steelhead Trout

Danielle Alvarez[1] and Rosi Dagit[1]*

[1] *Resource Conservation District of the Santa Monica Mountains, 540 S Topanga Canyon Blvd. Topanga, CA 90290*

Abstract.—Record drought from 2012 to 2016 followed by rainfall in the winter of 2017 provided an opportunity to examine how changing climate conditions may affect migration opportunities for the endangered southern steelhead trout (*Oncorhynchus mykiss*). This study examined how intermittently open estuary-ocean interfaces in the Santa Monica Bay that have historically supported steelhead evolved temporally and volumetrically. All seven lagoons in the study area breached by January 2017 after five years of drought and nearly exclusively closed conditions. Duration of breach was affected by the size of the lagoon, with smaller lagoons remaining breached longer than larger lagoons. Conversely, volume capacity persisted longer in larger lagoons. Lagoon condition was quantified by presence/absence of breach and passibility, coupled with daily rainfall. This study provides important lagoon planning, restoration and management information needed to support recovery of southern steelhead trout populations in the face of climate change.

Southern steelhead trout, *Oncorhynchus mykiss*, are a Distinct Population Segment (DPS) of west coast steelhead listed under the Federal Endangered Species Act (ESA) in August 1997. Historic stock numbers have drastically declined due to factors such as loss of estuarine habitat, land use practices that impact watershed function, and connectivity. More recently, the effect of extreme drought[1] that has affected rainfall and freshwater ecosystems across California from 2012 to 2016 has caused even more stress on these populations (NMFS 2016). Fewer than ten anadromous adults have been observed annually in the Southern California Distinct Population Segment region extending from San Luis Obispo to the Mexican border from 2014-2018.[2]

Restoration projects across the range of historic steelhead habitat in southern California, and in the Santa Monica Bay in particular, have helped remove documented passage barriers for migrating steelhead in recent years. It should be noted that passability as defined in this study refers specifically to the lagoon – ocean connection, whereas the ability of fish to move upstream from the lagoon through the mainstems of creeks is usually of much shorter duration and more difficult to document. Three passage barriers, including a check dam and two Arizona crossings, were removed over the course of three years in Arroyo Sequit Creek in Leo Carrillo State Park. This restoration was completed just before the rains of the 2016/2017 water year and resulted in the immigration of two anadromous steelhead trout (350 mm and 360 mm FL), the first anadromous individuals documented to return to the upper reaches of the creek since surveying began in 2004 (RCDSMM unpublished data). Similarly, the restoration of Lower Topanga Creek in 2009 and Malibu Lagoon in 2012-2013 have resulted in increased critical fish passage opportunities allowing three anadromous fish to migrate upstream from the ocean with the 2017 rains (RCDSMM unpublished data).

---

* Corresponding author: rosidagit@gmail.com

[1] USGS. 2017. US Drought Monitor: California Drought. Accessed 8/9/2017 droughtmonitor.unl.edu/CurrentMap/StateDroughtMonitor.aspx?CA.

[2] Nature Conservancy. 2018. California Salmon Snapshots, http://www.casalmon.org/salmon-snapshots.

Despite the success of restoration and anthropogenic passage barrier removal projects, natural passage barriers still exist for *O. mykiss* due to the nature of intermittently open bar-built coastal lagoons that are characteristic of Mediterranean climate regions, such as those in the Santa Monica Bay (McLaughlin et al. 2014). These “small creek” archetypal systems are identified as intermittently open bar-built estuaries.[3] According to the lagoon classification system by Jacobs et al. (2011)[4], the small, steep coastal creeks draining into the Santa Monica Bay respond similarly to the complex interactions of wave exposure, longshore transport, sediment delivery, watershed size, and formation processes. While historic data on creek mouths provided in the US Coast and Geodetic Topographic Survey (T-sheets) provides interesting information on past conditions, we found that due to extensive modifications over time, bar-built estuaries along the Santa Monica Bay needed to be further examined to better understand present constraints.

Lagoons not only provide important fish passage opportunities, but also can provide important foraging habitat for smolts - young trout migrating outward to the ocean (Bond et al. 2008). In central and northern California systems, the opportunity to spend time in brackish water adjusting to higher salinity levels also lowers stress levels for smolts during the freshwater to ocean transition (MacDonald et al. 1988). In order to support the recovery of southern steelhead trout, adequate connectivity is needed for immigration of anadromous adults to spawn and for juvenile smolts to migrate out to the ocean. If this exchange of habitat is unable to occur, gene flow and fecundity will continue to be reduced in the populations within the Santa Monica Bay, making them more susceptible to extirpation (NMFS 2012). The combination of current anthropogenic constraints caused by development adjacent to the creek mouths, impacts of Pacific Coast Highway and beach bar manipulation, muddle the behavior one would expect from examining past data and color restoration opportunities and constraints. This information will help us to understand how bar built estuaries in the Santa Monica Bay might respond to future climate change and sea level rise.

Systematic studies of the processes driving estuarine seasonal closure dynamics throughout Mediterranean zones worldwide provide some guidance, although observations of the patterns in southern California appear to be somewhat different than those observed elsewhere. McSweeney et al. (2017) developed a classification system for intermittently open/closed estuaries (IOCE) in Victoria, Australia, a Mediterranean climate like southern California. However, lagoons in Australia are tidally influenced, much larger in all ways, and unconstrained by topography so their behavior patterns differ. Northern California lagoons are much more exposed to wind and wave action due to their west facing orientation, yet many of the lagoons examined in northern California also breach naturally under lagoon-side flow driven processes instead of tidal processes (Kraus et al. 2008). A South African definition for estuaries also echoes processes seen in our study area. Describing a lagoon as "a coastal body of water in intermittent contact with the open sea and within which sea water is measurably diluted with fresh water from land drainage" (Day 1980), takes into account systems that may be dry for periods of time (Cooper 2001). This trait is seen in many of the lagoons in the Santa Monica Bay that dry down completely during summer/fall periods when rainfall is typically absent. Even when lagoon surface area persists through the dry season, connection between a lagoon and upstream habitat is often cut off beginning in the early summer due to subsurface flow in lower reaches (Dagit et al. 2017).

---

[3] Southern California Wetlands Recovery Project. 2018. Wetlands on the edge: the future of southern California's wetlands: Regional Strategy 2018. Prepared by the California State Coastal Conservancy, Oakland, CA.

[4] Jacobs, D., E. D. Stein, and T. Longcore. 2011. Classification of California estuaries based on natural closure patterns: Templates for restoration and management. Southern California Coastal Water Research Project Tech. Memo. 619:1-50.

Due to the low coastal exposure of the south/southwest facing beaches, lagoons of the Santa Monica Bay are not strongly influenced by wave action.[4] The Santa Monica Bay coastal area is situated facing south/southwest, which reduces the importance of wind action on beaches by diminishing strong wave action that contributes to longshore sediment processes that help deteriorate berms in higher wave exposure areas.[5] Dominant wave action is due to prevailing northwest winds during spring and summer months, with westerly winds that are common in fall through spring. However, south-southeast winter storm winds can sometimes generate strong waves that cause significant erosion. Overall, wave climate in the area is considered mild due to sheltering from deep ocean waves by the California Channel Islands, although west-facing beaches are more exposed to swell from storms in the North Pacific, and south facing beaches more susceptible to waves generated by southern swell. The lagoons east of Point Dume (including Solstice, Las Flores and Topanga), are generally more sheltered than those west of Point Dume (Zuma, Trancas, Arroyo Sequit and Big Sycamore). Waves greater than 3.5 m are most likely to erode sand from the beach, but these waves have not been found to occur often.[6] Instead, stream input and rainfall are the determining factor of breach potential and surface water presence. Stream flow, which is highly seasonal in California, is a major control on the state of a lagoon's inlet (Elwany et al. 1998).[4] Rich and Keller (2012) examined how watershed size and upstream slope can predict the behavior of small lagoons along the Santa Barbara Coast, determining that watershed size and the size of the associated lagoon are positively correlated.

Additionally, all the lagoons in the study zone are considered hydraulic estuaries that are normally closed to the sea during drier months by a bar that forms across the mouth of the lagoon.[4] Higher storm generated waves and higher tides both occur during the winter and, combined with higher flows associated with storm events, are associated with breaching the sand berms and re-connecting coastal creeks and lagoons with the ocean. Another characteristic that we did not specifically examine is tidal prism, the volume of water in a lagoon that is between mean high tide and mean low tide. Tidal prisms in river-dominated lagoons, where estuary side processes initiate breaches, are too small to maintain a breach against the wave action and tidal influence that the beach faces in the Santa Monica Bay typically receive (Cooper 2001). Like coastal exposure and formation process, tidal prism characteristics in the study area lagoons are defined more by morphological constraints that are uniform throughout the study area; additionally tidal prism is usually so small that it is not able to initiate breaches (Cooper 2001).

---

[5] Moffatt and Nichol. 2013. Broad Beach Restoration Project Coastal Engineering Report Exhibit L to CDP Application 4-12-043. Prepared for Broad Beach Geologic Hazard Abatement District.

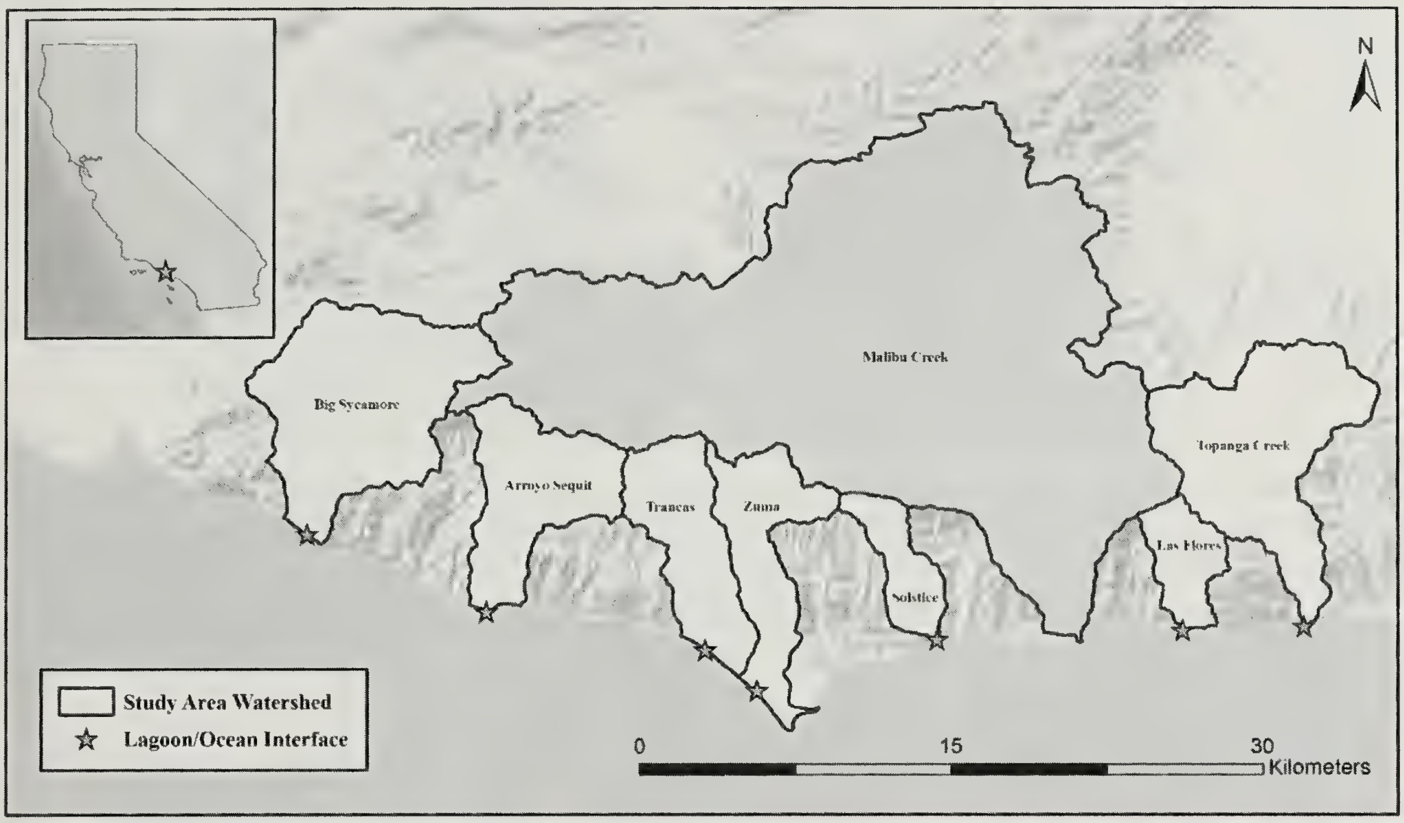
[6] Noble Consultants. 2009. Coast of California storm and tidal waves study, Los Angeles Region. Prepared for U. S. Army Corps of Engineers.

This study examined how intermittently open bar-built lagoon morphology, specifically breach frequency and volumetric changes, responded to rainfall after a period of drought, and the implications this may have on future restoration efforts to improve *O. mykiss* passage opportunities in the Santa Monica Bay. Seven lagoons within the Santa Monica Bay were selected for evaluation. Historically, Arroyo Sequit, Big Sycamore, Las Flores, Malibu, Solstice, Topanga, Trancas, and Zuma Creeks all supported southern steelhead trout populations (NMFS 2012), but current lagoon conditions restrict passage opportunities at all but Malibu Creek, which was restored in 2012. Malibu Creek is the only antecedent creek that crosses the Santa Monica Mountains from the San Fernando Valley to the ocean; its course remained the same and cut through bedrock despite the uprising of the Santa Monica Mountains. Malibu Creek also receives extensive imported water flows. Due to the recent restoration actions undertaken at this lagoon and its differences from the other coastal creeks, which do not experience either significant inputs of imported water or withdrawal of groundwater resources, Malibu is not further considered in this study. The baseline in-depth data provided for the seven lagoons in this study provide critical context for land use managers and restoration planners as the systems in our study have been identified as a priority watersheds for restoration (NMFS 2012).

Materials and Methods

Based on the watersheds identified in the Southern California Steelhead Recovery Plan (NMFS 2012), the following lagoons and creeks within the Santa Monica Bay were the focus of this study: Arroyo Sequit, Big Sycamore, Las Flores, Solstice, Topanga, Trancas, and Zuma. Although Malibu Creek is the second largest watershed draining into the Santa Monica Bay with present and historic southern steelhead trout habitat, Malibu lagoon was not included in this analysis. Due to the augmentation of flow from Tapia Water Reclamation Facility's discharge in accordance with California Regional Water Quality Control Board Los Angeles Region's NPDES NO. CA0056014, Malibu Creek and lagoon are the only system within the Santa Monica Bay that has a significantly altered hydrologic profile. All the other lagoons and their associated creeks rely on streamflow provided by natural variables such as rainfall and/or the water table. Regional context of these watersheds within the Santa Monica Mountains National Recreation Area and Santa Monica Bay (Fig. 1), along with individual watershed boundaries and limits of anadromy (Fig. 2) for all the study watersheds and lagoons are important to note when considering anthropogenic alterations. All of the systems in our study area have been altered in some way, changing the length of stream available for southern steelhead trout and imposing lagoon constraints due to Pacific Coast Highway (PCH) bridges (Table 1). Other anthropogenic factors include channelization in creek reaches, concrete culverts, multiple bridge constraints, Arizona type instream crossings, and fully restricted lagoons by wall or riprap barriers.

Rainfall metrics were obtained using LA County Department of Public Works, Water Resources Division's "Precipitation" webpage (http://www.ladpw.org/wrd/precip/). Using the "Near Real-Time Precipitation Map", and gauges with closest proximity, daily rainfall was calculated for each lagoon's watershed. The Lechuza gauge (# 454) data was used for Arroyo Sequit, Big Sycamore, Trancas and Zuma watersheds. The Big Rock Mesa



Service Layer Credits: Sources: Esri, USGS, NOAA

Fig. 1. Watershed boundaries of the northern Santa Monica Bay.

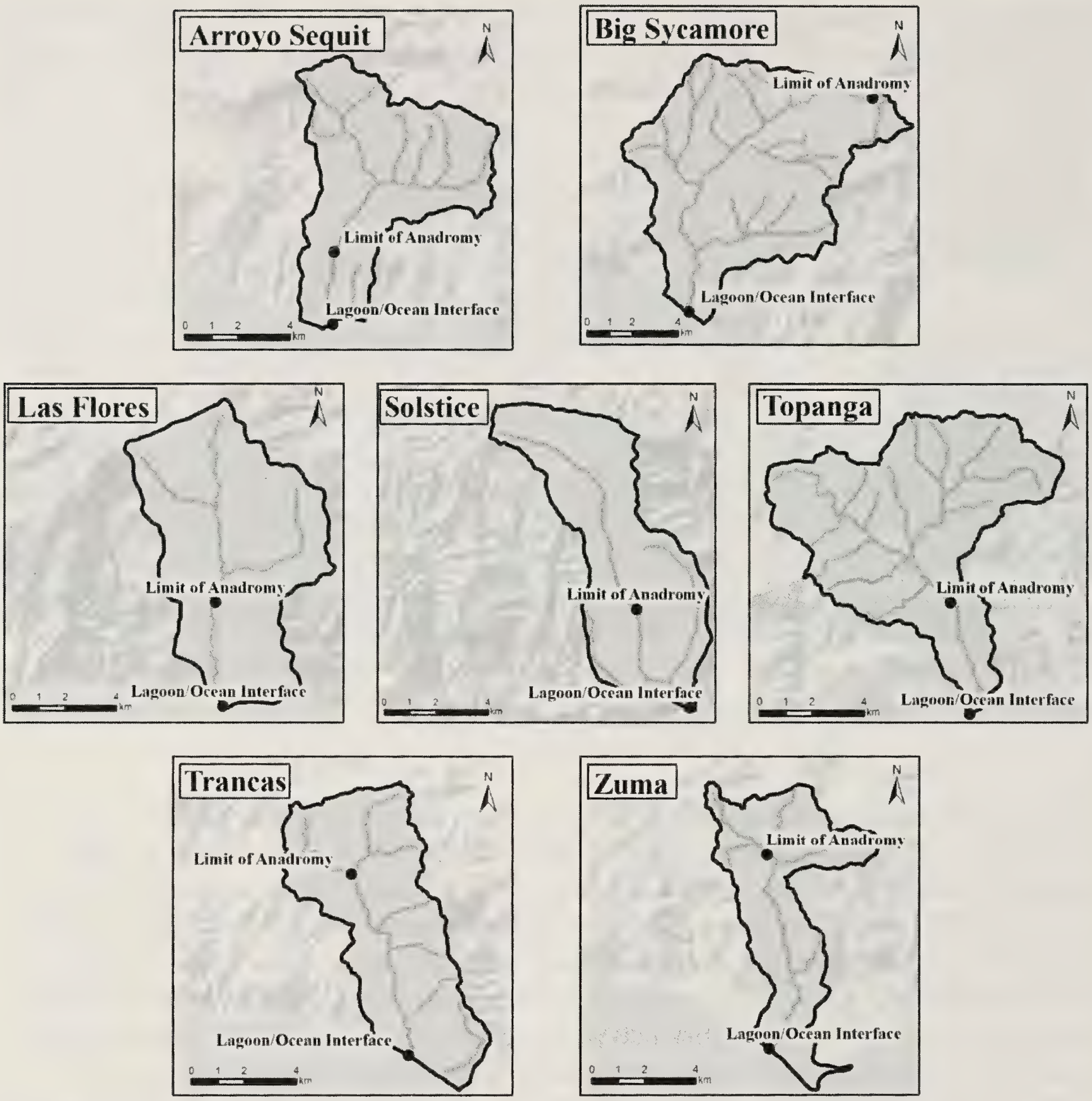
gauge (#320) was used for Las Flores watershed, the Monte Nido gauge (#319) was used for Solstice watershed, and the Topanga Canyon gauge (#318) was used for Topanga watershed. Flow data was obtained for Topanga Creek from the Topanga surface water flow gauge (F54C) maintained by Los Angeles County. Data was available for 2013-2017, but due to changes in thalweg location, the gauge currently sits a couple meters away from the thalweg and does not capture any low flow measurements, despite flow being present. Although we recognize the importance of flow, because this data was so limited and not available for all creeks, it was not incorporated further in this study.

Overwash from high tides and storm event tides can affect passage opportunities for southern steelhead trout into the study area's lagoons. Tide data for the 2013-2017 study period was measured at Los Angeles Station ID: 9410660, (33.7200, -118.2720). Because

Table 1. Descriptive measurements of each lagoon and watershed.

Location	Watershed/ Catchment Area	Limit of Anadromy	PCH Hwy Culvert Dimensions	Mean Annual Rainfall[*]	Coastal Exposure	Average Lagoon Wetted SA, 2017
Arroyo Sequit	31km^2	2.64rkm[!]	24.2m x 23.75m	14.094	Low	963.3 m^2
Big Sycamore	54.4km^2	19.3rkm	16.8m x 23.2m	14.094	Low	2009.67 m^2
Las Flores	11.7km^2	3.2rkm	16.6m x 27.7m	11.874	Low	557 m^2
Solstice	11.1km^2	3.2rkm	7.17m x 43.02m	13.126	Low	140.33 m^2
Topanga	46.6km^2	5.3rkm	19.7m x 27.5m	11.2	Low	4561.33 m^2
Trancas	26.4km^2	10.46rkm	30.5m x 25.8m	14.094	Low	1995.67 m^2
Zuma	25.9km^2	8.05rkm	30.4m x 23.4m	14.094	Low	9624.33 m^2

[*] Mean annual rainfall calculated by averaging rainfall from 2013-2017 water year data collected.
[!] Limit of anadromy under low flow conditions.



Service Layer Credits: Sources: Esri, USGS, NOAA

Fig. 2. Individual Watershed boundaries and creek locations.

we describe breach frequency when the connection was both passable and not passable, passable conditions were augmented for times when high tide could allow passage. When a lagoon was breached, any tides over 1.52 m above Mean Low Low Water (MLLW), were noted for potentially passable connection during high tide.

Four comprehensive longitudinal profile lagoon surveys occurred in November 2013 and January, June, and October 2017 at all sites. Lengths and widths of wetted area were recorded at wetted cross sections using hand held 100-meter tapes. Garmin GPS units recorded waypoints of lagoon boundaries (DATUM: WGS84) and GPS locations were uploaded into Google Earth. Lagoon area polygons were then mapped using the waypoints, observable landmarks (such as the PCH bridges), and survey notes. Storm-event related monitoring of the lagoon/ocean interface was conducted from October 2013 through December 2016 in order to document passage opportunities and constraints. In response to large and frequent storms starting in January 2017, weekly lagoon monitoring was conducted by a field team of two or three surveyors. These surveys consisted of visual documentation of lagoon and breach conditions via field notes and photo points to record physical condition (depth, connectivity, etc.) changes over time. Passibility was also recorded at the time of these surveys. Any connection between the lagoon and the ocean, even a steady connected trickle, was considered a breach. Only when flow was of adequate depth and size was the breach considered and noted as passable. A connection was considered passable if there was at least 15-30 cm of depth in the connection between the ocean and lagoon.[7] It is possible for a connection to be passable only at high tide, which was difficult to assess in our surveys since each site was assessed at varying times throughout the tidal cycle. Subsequently, a lagoon was only marked passable if it was clearly accessible at the time of survey. Later tide analysis was performed to predict additional potentially passable opportunities at high tide, a roughly 1-3 hr window. When a lagoon was breached, any tides over 1.52 m (MLLW), were examined for passable connection during high tide. Data from less frequent breach condition surveys from 2013-2016 was included for temporal context.

Field measurements of the lagoons documented conditions in January, June, and October 2017; at the beginning of rains, the beginning of summer, and the end of the water year when the lagoons have been subjected to the entire dry season. Physical measurements were then mapped in Google Earth to create a visual time series of lagoon dimensions and to obtain temporal descriptive measurements of lagoon wetted surface area (SA) and volume (V). SA and V from November 2013 was included in tables for context but not included in analysis since survey methods and measurements were not consistent with the surveys conducted in 2017. Average depths were estimated based on multiple depth measurements taken with a meter stick throughout each lagoon, but this method could be improved by using water level data loggers that would give a continuous timeline of changing lagoon depth over time. This method was not utilized in this study due to limited funding for such loggers.

All data was entered by date and location. Graphs of lagoon breach condition in relation to rainfall on a temporal scale were created for each lagoon. Lagoon volume was calculated by mapping lagoon boundaries via Google Earth mapping software, creating polygons to the specific measurements calculated and recorded in the field. Surface area calculations were coupled with average depth measurements recorded during survey visits to calculate an estimated volume at that particular point in time. An observed rate of rainfall required to cause a breach was calculated by taking the total amount of rain fallen in the watershed from October 1st to first day of breach for each lagoon and dividing it by the number of days until first breach, $\frac{centimeters\ of\,rain}{\#\ of\ days\ until\ 1st\ breach}$. Statistical analysis was performed using JMP statistical software. Continued surveys following the same methods may provide a data set large enough to perform robust statistical analysis in the future.

Results

In the 2016-2017 water year, rainfall throughout the Santa Monica Bay averaged 65.79 cm. Rain data for each watershed can be found in Table 2. Rain data was used to calculate several variables that were used for volume and breach frequency analysis.

---

[7] Flosi, G., and F. L. Reynolds. 2010. California salmonid stream habitat restoration manual. Second edition. California Department of Fish and Game, Sacramento, CA. http://www.dfg.ca.gov/fish/Resources/HabitatManual.asp.

Table 2. Watershed and rain characteristics of study area for the 2017 water year.

Location	Watershed Area (km^2)	2017 Rainfall (cm)	Watershed Rain Volume (m^3)	Rain Rate (cm/day)
Arroyo Sequit	31	73.81	22,881,800	0.092
Big Sycamore	54.4	73.81	40,153,900	0.162
Las Flores	11.7	56.21	6,576,590	0.076
Solstice	11.1	62.9	6,992,110	0.069
Topanga	46.6	67.03	31,236,300	0.056
Trancas	26.4	73.81	19,486,500	0.082
Zuma	25.9	73.81	19,117,400	0.148

These include the volume of rain fallen (watershed area multiplied by rainfall) over each watershed during the 2017 water year and rain rate, defined in this study as centimeters of rain per day until first breach.

Topanga Creek is the only system that has a flow gauge, but it is currently located in a position that does not accurately measure low flow conditions. According to the available data, Topanga Creek had a mean daily discharge of 0.11 m^3/s, a maximum of 1.66 m^3/s, and a minimum of 0 m^3/s for the 2017 water year. Average daily discharge was 0.024 m^3/s for the 2012 water year, 0.021 m^3/s for 2013, 0.017 m^3/s for 2014, 0.027 m^3/s for 2015, and 0.023 m^3/s for 2016. No flow data was available for any other site. A conceptual hydrology analysis estimated flow rate in cubic feet per second for Trancas lagoon for several potential lagoon restoration alternative designs. Depending on lagoon restoration area size, determined that a two-year storm could produce flows between 0.007-0.033 m^3/s, while a ten year storm could produce flows between 0.028-0.282 m^3/s.[8]

All lagoons showed a time lag between end of breach and end of observed overwash, an expected observation as sediment deposition to rebuild a berm takes several days to weeks, depending on the specific location. Seaward wave action, already of low influence for the study area, became less of a factor on breach potential when a berm barrier was high and wide. When accounting for tidal influence, the amount of time of passable connection was increased by tides when a system was breached. Recorded days of full passibility for each lagoon can be found in Table 4. Due to funding constraints, it was not possible to measure tidal prism as part of this study.

All the lagoons – with the exception of Topanga – were consistently dried down almost completely between 2013 and 2016, highlighting the severity of the California drought (Table 3). Arroyo Sequit had a modest volume throughout the 2017 water year with a maximum of 821 m^3 in June 2017. Volume in Big Sycamore measured less than 100 m^3 during both November 2013 and January 2017 survey, and then increased more than a factor of 20 by June 2017. Anthropogenic constraints limited any lateral movement of water in Las Flores and resulted in a maximum volume of only 337 m^3. Similarly, constraints on Solstice Lagoon from the PCH culvert and manipulation by individuals (placing sand bag, digging small trenches) resulted in a small maximum volume of 125 m^3. Trancas Lagoon had a dramatic volumetric change, quadrupling in wetted surface area and doubling in estimated depth throughout the study period. Topanga lagoon held onto its surface water the longest

---

[8] Dagit, R., S. Albers, and C. Stevens. 2015. Trancas lagoon restoration feasibility study 2013-2015. Prepared for CDFW and Zuma Beach Properties, LLC. Resource Conservation District of the Santa Monica Mountains, Topanga.

Table 3. Recorded lagoon surface area, depth, and volume including changes in measurements between November 2013, January 2017, June 2017, and October 2017 surveys.

Location	Date of Survey	Wetted Area	ΔWetted Area	Average Depth	ΔAve Depth	Estimated Volume	Δvolume
Arroyo Sequit	11/1/2013	0		0		0	
	11/1/2014	0	0	0	0	0	0
	11/1/2015	0	0	0	0	0	0
	11/1/2016	0	0	0	0	0	0
	1/27/2017	1064	1064	0.55	0.55	585.2	585.2
	6/23/2017	1561	497	0.53	-0.02	821.65	236.45
	10/1/2017	265	-1296	0.41	-0.12	108.65	-713.00
Big Sycamore	11/1/2013	268		0.33		89.04	
	11/1/2014	0	-268	0.00	-0.33	0.00	-89.04
	11/1/2015	0	0	0.00	0	0.00	0
	11/1/2016	0	0	0.00	0	0.00	0
	1/27/2017	569	569	0.1	0.10	56.9	56.90
	6/23/2017	3011	2442	0.68	0.58	2048.27	1991.37
	10/1/2017	2449	-562	0.64	-0.04	1561.24	-487.03
Las Flores	11/1/2013	278		0.32		88.96	
	11/1/2014	0	-278	0	-0.32	0	-88.96
	11/1/2015	0	0	0	0	0	0
	11/1/2016	0	0	0	0	0	0
	1/27/2017	292	292	0.3	0.3	87.6	87.6
	6/23/2017	730	438	0.46	0.16	337.63	250.03
	10/1/2017	649	-81	0.1	-0.36	64.9	-272.73
Solstice	11/1/2013	0		0	0	0	0
	11/1/2014	0	0	0	0	0	0
	11/1/2015	0	0	0	0	0	0
	11/1/2016	0	0	0	0	0	0
	1/27/2017	222	222	0.3	0.3	66.6	0
	6/23/2017	177	-45	0.71	0.41	124.96	58.36
	10/1/2017	22	-155	0.55	-0.16	12.1	-112.86
Trancas	11/1/2013	751		0.34		252.84	
	11/1/2014	0	-751	0.00	-0.34	0.00	-252.84
	11/1/2015	0	0	0.00	0	0.00	0
	11/1/2016	0	0	0.00	0	0.00	0
	1/27/2017	898	898	0.3	0.30	269.4	269.40
	6/23/2017	4419	3521	0.7	0.4	3093.3	2823.9
	10/1/2017	670	-3749	1.1	0.4	737	-2356.3
Topanga	11/1/2013	3453		0.75		2589.75	
	11/1/2014	No Data	No Data	No Data	No Data	No Data	No Data
	11/1/2015	No Data	No Data	No Data	No Data	No Data	No Data
	11/1/2016	No Data	No Data	No Data	No Data	No Data	No Data
	1/27/2017	4298	No Data	0.1	-0.65	429.8	No Data
	6/23/2017	5334	1036	0.75	0.65	4000.5	3570.7
	10/1/2017	4052	-1282	0.75	0	3039	-961.5
Zuma	11/1/2013	813		0.16		130.08	
	11/1/2014	0	-813	0	-0.16	0	-130.08
	11/1/2015	0	0	0	0	0	0
	11/1/2016	0	0	0	0	0	0
	1/27/2017	10148	10148	1.5	1.5	15222	15222
	6/23/2017	11004	856	1.2	-0.3	13204.8	-2017.2
	10/1/2017	7721	-3283	1	-0.2	7721	-5483.8

into the drought with some surface water consistently present (no surface area/volume measurements available) through 2014-2016 and an increase in volume measuring 4000 m^3 during the June 2017 survey. Zuma lagoon was the quickest to recover from drought conditions, drying down almost completely from 2014-2016 and then increasing to an estimated volume of 15,222 m^3 in the January 2017 survey.

Throughout the 2017 water year, a trend in volume changes was observed. Apart from Big Sycamore, all lagoons had a small volume in January 2017 when all lagoons were breached and outflowing, recorded their largest volume measurement in June 2017, and measured the smallest volume in October 2017 because of dry down from high summer temperatures. Big Sycamore was the only location that had a larger volume in October 2017 than in January 2017. Lagoon depth was extremely variable throughout the study area. Some locations increased in depth between each survey in 2017 (Trancas and Topanga); some locations decreased in depth between each survey (Arroyo Sequit and Zuma); and some locations increased depth between January and June, then decreased in depth between June to October (Big Sycamore, Las Flores, Solstice). Fig. 3 and Fig. 4 illustrate the changes in lagoon volume over time at each location in this study. Some mapped surface areas in Fig. 3 appear to extend into the surf. GPS data for these instances were verified for accuracy. Though all surveys were conducted during the day in the same order, some occurred during low tide times, which explains the appearance of some of the maps extending into the ocean. 27 January 2017 was the day of the new moon so neap tides were experienced with an afternoon low tide of 0.027m below MLLW.

Anthropogenic factors affect all the study locations and influence the volume capacity in some way. Instream creek barriers in Arroyo Sequit were recently restored, but the PCH bridge, a concrete pedestrian walkway, and a vehicle driveway line the edges of the lagoon, confining its footprint. Big Sycamore is under similar constraints with a pedestrian bridge running across the upper portion of the lagoon and the PCH bridge along the lower end where riprap holds the banks in place between these two bridges. Las Flores is bordered on either side by tall concrete retention walls with buildings on the east bank, and Solstice has a long culvert under PCH which causes sheet flow into the lagoon and cuts off any upstream migration possibility. Topanga also suffers from constraints due to the concrete retention walls extending from the PCH bridge and fill slopes to a regularly groomed berm. Unlike the other lagoons with more natural channels upstream of the mouth, Trancas Creek has a 600 m concrete trapezoidal flood control channel that begins upstream of the lagoon and channels flow in a way that may affect lagoon morphology. Zuma lagoon has the most unconstrained banks and is by far the largest in our study, but multiple Arizona crossings, regular grooming to maintain the berm for lifeguard vehicle access, and vector control manipulation within the lagoon itself all affect its suitability as potential *O. mykiss* habitat.

Increasing lagoon volume correlated with higher surface areas in the study area lagoons ($R^2 = 0.897$, $p \leq 0.001$). Due to the multi-year drought, all lagoons effectively started the 2016-2017 water year almost completely dry, but the ensuing 2017 rainy season increased surface flows and restored passable conditions into the upper reaches of each system. Santa Monica Bay lagoons with bigger surface areas were more likely to contain a larger volume of water (Fig. 5). There was no significant relationship between watershed area and lagoon surface area. Controlling for differences in rain received over different watersheds in the study area, total rainfall for the 2017 water year was couple with watershed area to get a volume of rain fallen within each watershed (Table 2). Watershed volume in relation to lagoon surface area yielded no significant relationship. A more robust sample size in the

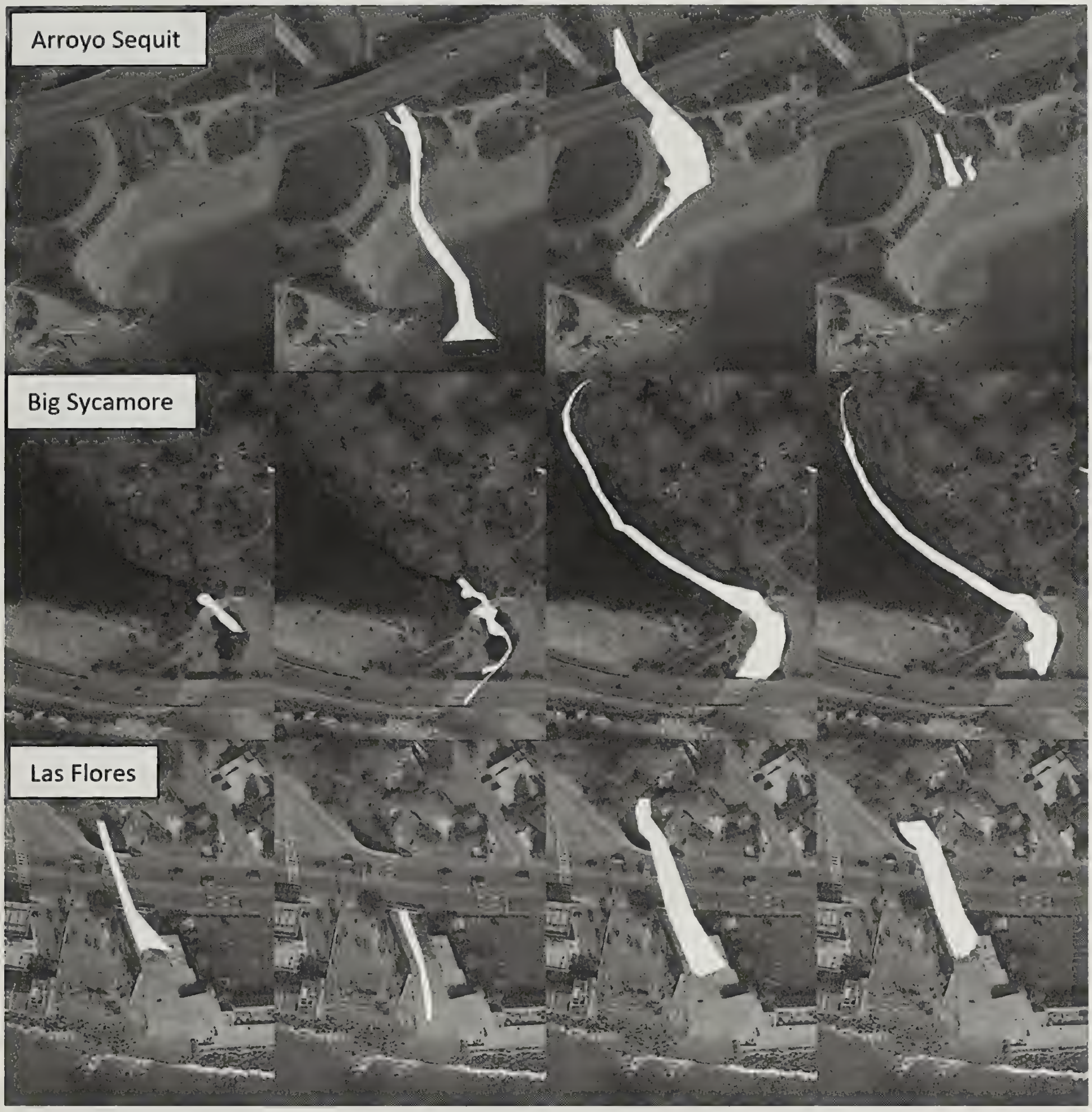


Fig. 3. Mapped surface area of Arroyo Sequit, Big Sycamore, and Las Flores lagoons on surveys conducted on 3 November 2013, 27 January 2017, 23 June 2017, and 5 October 2017 (maps ordered chronologically from left to right). *Las Flores Lagoon dried down completely when observed a week prior to the 5 Octobe4 2017 survey. County employees bulldozed the lagoon, removing all in-channel vegetation as well as several inches of sand revealing sub-surface water that was not previously exposed.

future would improve the confidence in our analysis and be a better indicator of the true relationship between catchment area and lagoon size. Fig. 6 shows how depth in the study area lagoons evolved during a year of average rainfall following a multiyear drought. Depth peaked in the middle of the year, when rains had ceased but before the peak in average high temperatures that Southern California experiences from July to September each year.[9]

A summary of storm events, breaches, and possible fish passage opportunities is provided in Table 4. Passable connection was defined as a breach with enough depth for

---

[9] US Climate Data 2018, Climate – Los Angeles. https://www.usclimatedata.com/climate/los-angeles/california/united-states/usca1339.

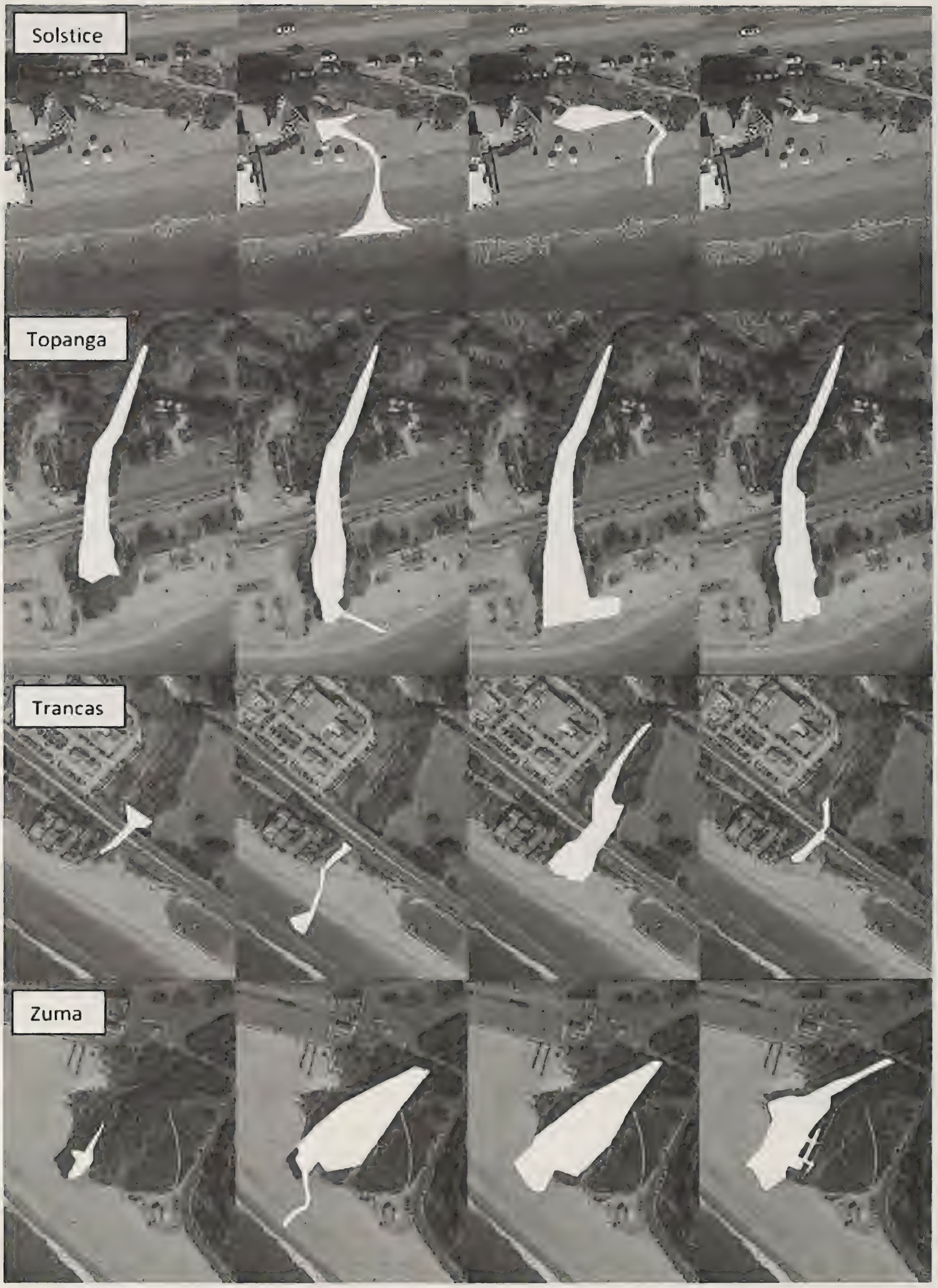


Fig. 4. Mapped surface area of Solstice, Topanga, Trancas, and Zuma lagoons on surveys conducted on 3 November 2013, 27 January 2017, 23 June 2017, and 5 October 2017 (maps ordered chronologically from left to right).

Table 4. Summary of rainfall and fish passage opportunities of monitored lagoons in the Santa Monica Mountains, in alphabetical order.

Lagoon	Water Year*	Rainfall Total** (inches)	Dates Entrance Open	Number of Days Breached	Estimated Number of Days Passable to *O. mykiss*	*O. mykiss* present
Arroyo Sequit	2013-2014	5.87	unknown	0	0	Yes
	2014-2015	17.5	none	0	0	Yes
	2015-2016	9.09	29 Oct 2015	1	1	Yes
	2016-2017	29.06	30 Dec 2016- 14 Jan 2017 18 Jan – 8 Apr 2017	97	51	Yes
Big Sycamore	2013-2014	5.87	none	0	0	No
	2014-2015	17.5	03 Mar 2015 (trickle) 29 October 2015 (storm)	0	0	No
	2015-2016	9.09	none	0	0	No
	2016-2017	29.06	23 – 27 Jan 2017 3 Feb – 8 Mar 2017	39	30	No
Las Flores	2013-2014	5.16	26 Feb – 02 Mar 2014	4	4	No
	2014-2015	17.12	12 Dec 2014 – 3 Mar 2015 (pinched)	10	<10	No
	2015-2016	7.36	6 – 12 Mar 2016	7	1	No
	2016-2017	22.13	24 Dec 2016 – 21 Apr 2017	119	44	No
Solstice	2013-2014	6.31	none	0	0	No
	2014-2015	16.06	12 – 16 Dec 2014 12 Jan 2015	7	<10	No
	2015-2016	9.84	5 – 15 Mar 2016	11	0	No
	2016-2017	24.8	23 Dec 2016 – 3 Jul 2017	193	5	No
Topanga	2013-2014	6.84	27 Feb – 07 Mar 2014 25 March 03 Dec and 12-16 Dec 2014	10	4	Yes
	2014-2015	13.76	10 – 19 Jan and 3 Mar 2015 03 Mar 2015	17	<10	Yes
	2015-2016	8.31	6 March – 6 April 2016	32	5	Yes
	2016-2017	26.39	21 – 26 Dec 2016 11 Jan – 16 May 2017	132	36	Yes
Trancas	2013-2014	5.87	none	0	0	No
	2014-2015	17.5	3-8 Dec 2014 (overwash) 16 Dec 2014 (pinched)	5	<5	No
	2015-2016	9.09	6 Mar 2016	1	0	No
	2016-2017	29.06	24 Dec 2016 – 12 Jan 2017 19 Jan – 18 Apr 2017	110	61	No
Zuma	2013-2014	5.87	none	0	0	No
	2014-2015	17.5	none	0	0	No
	2015-2016	9.09	none	0	0	No
	2016-2017	29.06	20 Jan – 1 Mar 2017	41	39	No

** Water year, as used by the USGS: October 1 through September 30 of the following year.*

*** Rainfall data from gauge stations managed by Los Angeles County Department of Public Works.*

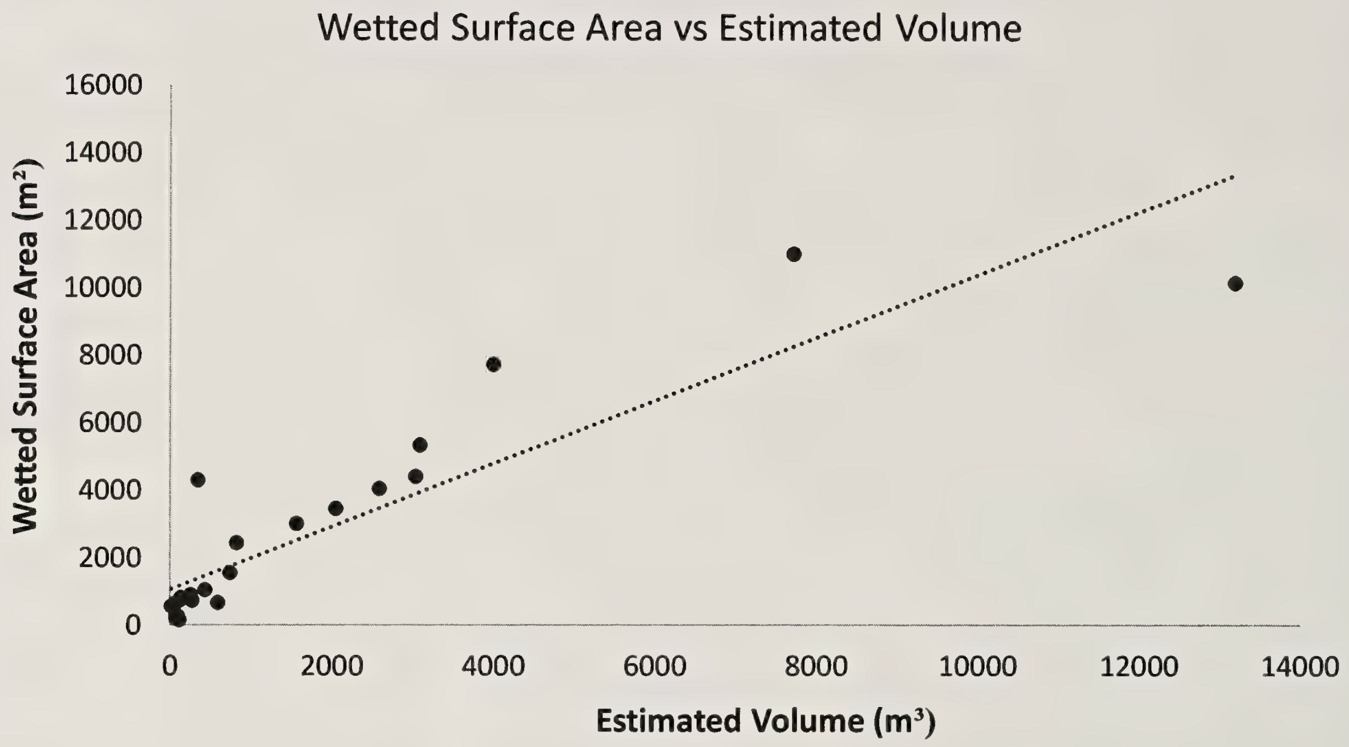


Fig. 5. Wetted surface area measurements are positively associated ($p < 0.001$) with increased volumes for all lagoon surveys conducted post-rain in 2017.

O. mykiss to migrate to or from the ocean to the lagoon during all tides. Breach patterns for lagoons with larger surface areas such as Big Sycamore and Topanga were strongly influenced both by rain events and by the constraints of the PCH bridges and fill slopes that border these lagoons. Breaches closed rapidly after storms in the beginning of the

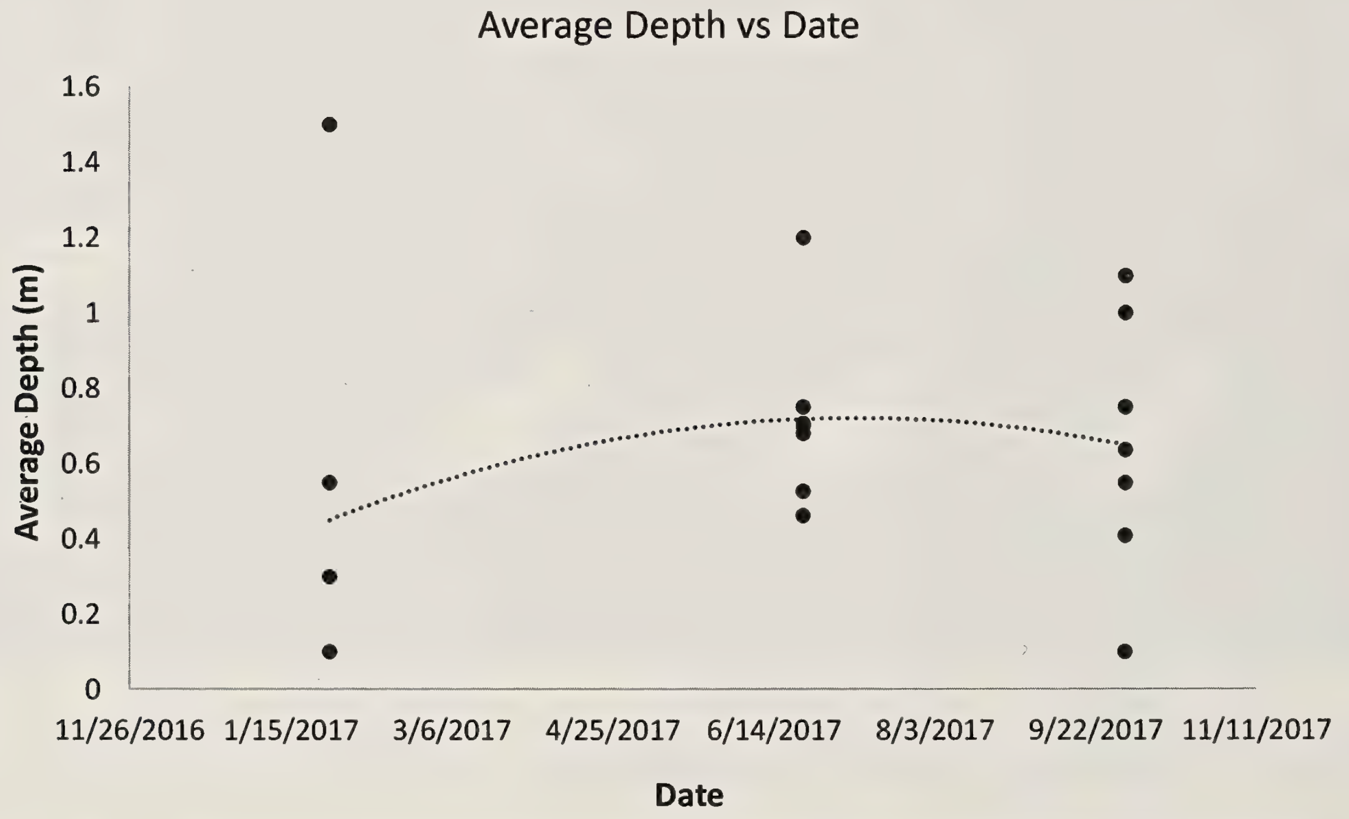


Fig. 6. Average depth measurements of each lagoon during 27 January 2017, 23 June 2017, and 5 October 2017 survey. Includes mean depth (line curve; cm) and confidence of fit (background shading).

season, but once reopened, the lack of ability to spread out helped sustain subsequent breaches. Zuma lagoon was more influenced by rain events, as this location lacked lagoon bank constraints. It took less cumulative rainfall to cause a breach in Topanga and Big Sycamore than in Zuma, but once breached, Zuma's connectivity to the ocean was sustained. Breaches for the lagoons with smaller footprints tended to occur more quickly during the rainy season and lasted for months. Small windows of closure occurred in Arroyo Sequit and Trancas, but they did not close for long. It should be noted that passibility in this study refers specifically to the lagoon–ocean connection, whereas the ability of fish to move upstream from the lagoon through the mainstems of the creeks is usually of much shorter duration and more difficult to document. Documented windows of passibility during a site visit, when a breach was clearly passable for *O. mykiss,* were recorded and later analysis of tides resulted in an estimation of possible passable windows during high tide to give a detailed evolution of breach at each location over the span of the 2017 water year (Fig. 7). No relationship was identified between watershed volume and number of days of passable connection. There was more significance to the relationship between watershed volume and the number of days a system was breached.

The open period for all lagoons ranged from 39 d (10.68% of the year) to 193 d (52.88%) in the 2016-2017 water year, with an overall average time breached at 104 d (28.61%). Comparing the number of days breached with the average lagoon surface area measured on 27 January, 23 June, and 5 October 2017, there was a slight trend showing that larger surface area lagoons were open for fewer days, and smaller surface area lagoons were open for more days over the water year. Since the surface area values for each location were averaged between the three survey events, there are only seven data points to work with and no significance was calculated in this relationship.

Calculated rain rates ranged from 0.143 to 0.412 cm/d with a median of 0.221 cm/d. Comparing the rate of rainfall/d needed for first breach by the average lagoon surface area as measured on 27 January, 23 June, and 5 October 2017, larger lagoons needed more rain to initiate first breach, whereas smaller lagoons were able to breach with less accumulated rainfall. When examining the effects of lagoon surface area and watershed volume on rain rate needed for first breach (Fig. 8), both were positively correlated. Increasing average surface area or watershed volume predicted an increase in rain rate (i.e. an increased amount of rain required for first breach to occur), though linear regression revealed a higher confidence in the line of best fit between rain rate and watershed volume. A significant negatively correlated relationship between rain rate and the number of days a system was breached was discovered. Locations that were breached the longest also had lower rain rates, while shorter breach windows required a higher rain rate ($R^2 = 0.763$ and $p = 0.01$).

Discussion

Restoration planning is in progress for many of the lagoon systems in the Santa Monica Bay and design for these efforts not only must account for site-specific conditions, but also address regional wetland restoration and species recovery goals. When considering restoration options, it is critical to evaluate the implications of lagoon size because breaching frequency may depend on it (Rich and Keller 2012). Data on the presence/absence of steelhead, as well as information regarding the existing lagoon breach patterns, was compiled in order to identify the appropriate regional archetypes and lagoon classification patterns, which can help guide restoration designs. The challenge for restoration planners is to provide the right balance between connectivity during the winter months when stream

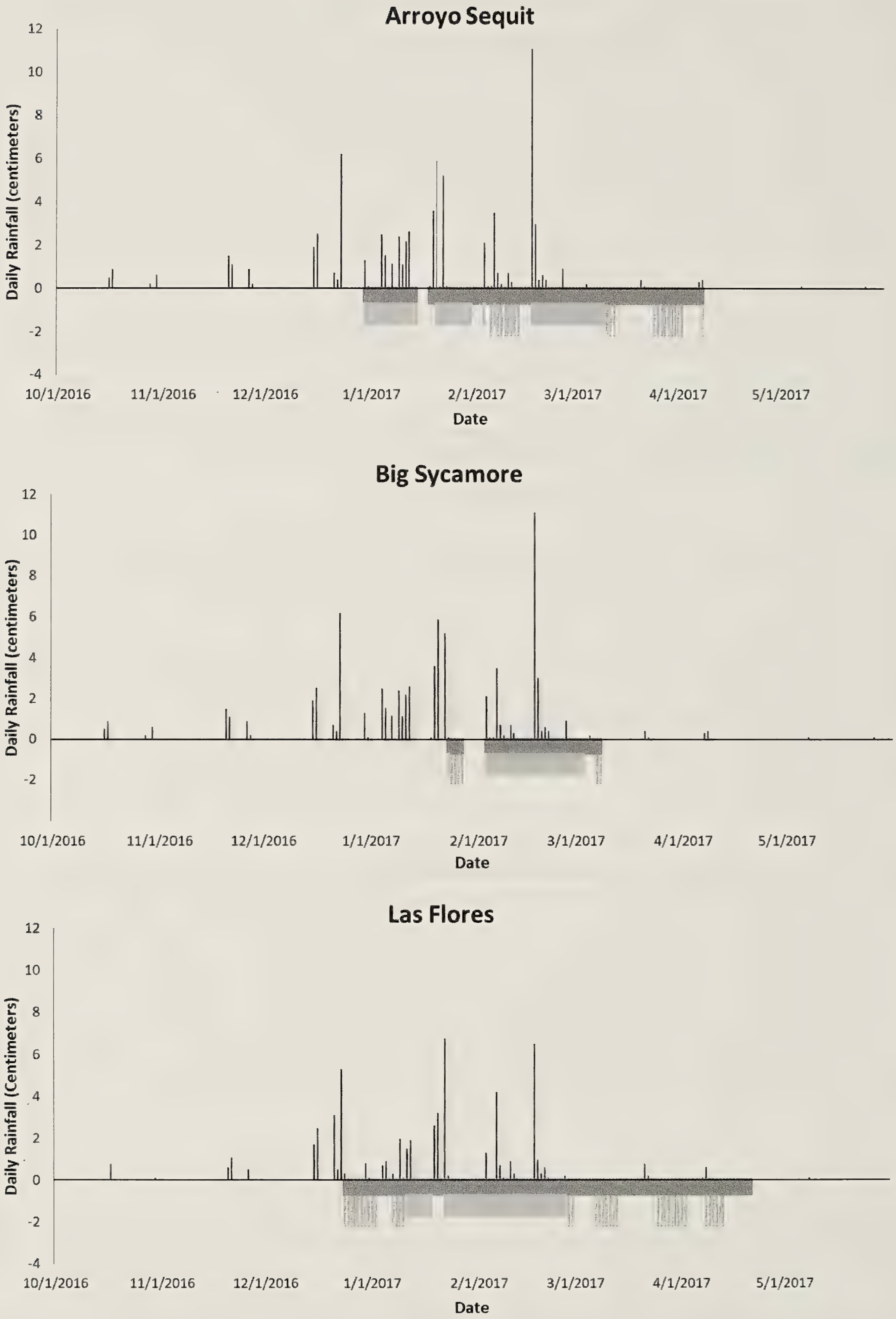


Fig. 7. Lagoon breach condition related to rainfall over the 2017 water year. (Breach = dark grey bar; Passable Connection = light grey bar; Rainfall = dark line columns).

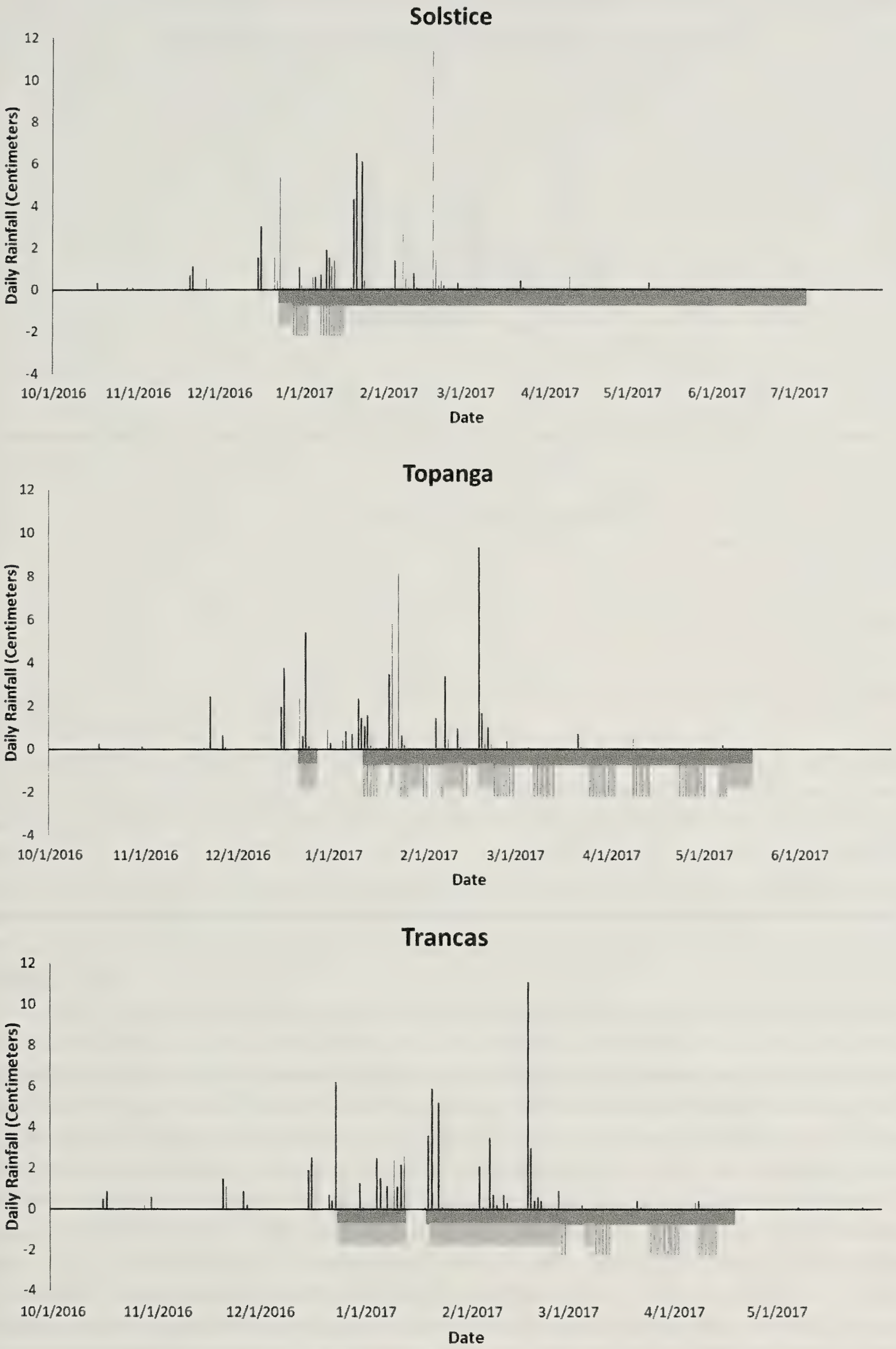


Fig. 7. Continued.

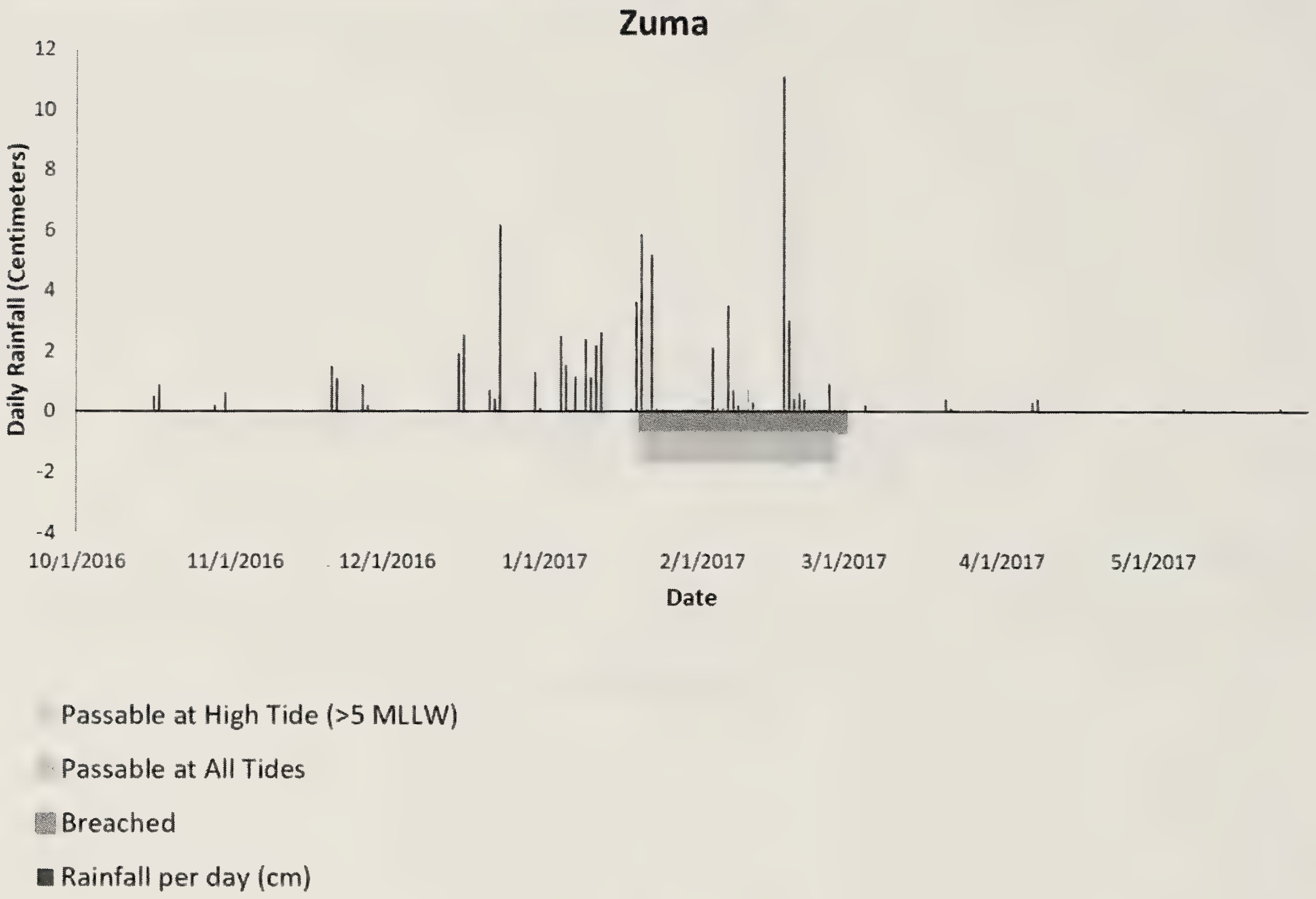


Fig. 7. Continued.

flows typically drive lagoon breaches (McLaughlin et al. 2014)[4], versus accommodating more wetland habitat and transition zones that will provide flexible response to projected and measured sea level rise (Nerem et al. 2018). When stream flow is a limiting factor, the general assumption that larger systems remain open for longer periods of time when compared to their smaller counterparts was not observed during our study.[4]

All seven of the lagoon-creek systems examined in this study fit the "small creek" archetype, and while similar patterns were observed in regard to breach dynamics, further classification was confounded by the unique constraints particular to each system. Rich and Keller's (2012) analysis of small coastal lagoons near Santa Barbara, CA, a similar coastal area, found that the size of an estuary was directly related to watershed size. In their study, larger watersheds produced larger creek channels which in turn resulted in larger lagoons. While this relationship could not be confirmed in our study area, other observations from locations with similar characteristics were also seen in the Santa Monica Bay. As has been observed in several Mediterranean regions, breaching was initiated by processes on the lagoon side of the berm, namely the lagoon/ocean water elevation difference and the width of the barrier beach (Kraus et al. 2008). Berm closure was initially caused by wave driven sediment import that occurred at a rate slightly higher than sediment export from tides and creek flow (FitzGerald 1996). Behrens et al. (2013) also observed that the amount of closed days is more dependent on river flow and less related to wave condition. These observations closely match the patterns documented in this study. Despite differences in volume capacity, the drought reduced the lagoons in our study area to meager puddles or completely dry channels that no *O. mykiss* were able to access for years. Evaporation rates and water seepage due to the porosity of substrate are factors that can contribute to lack of surface water in lagoons, and the lowering of the water table likely

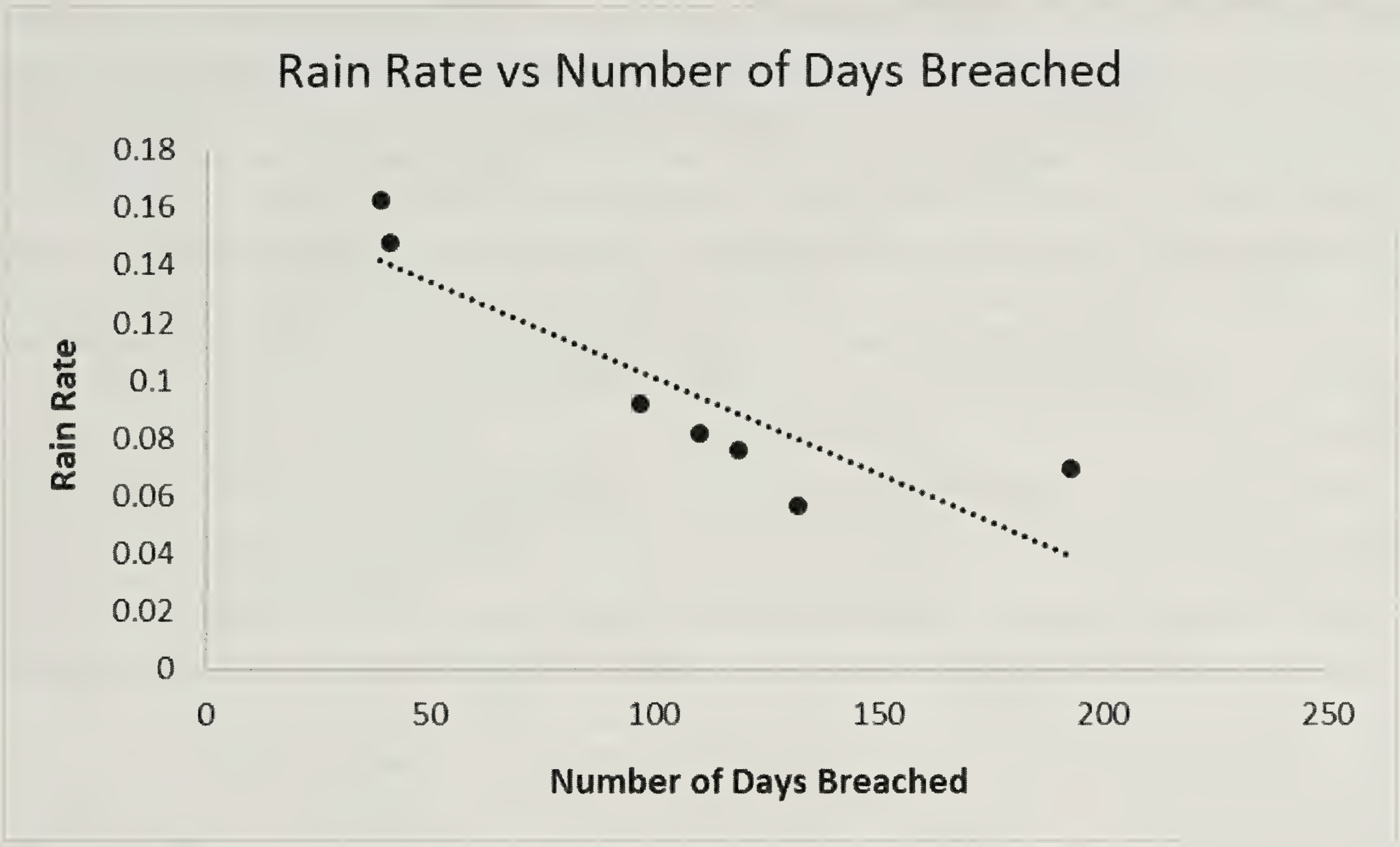


Fig. 8. Rate of rain/d versus number of days breached.

contributed to an overarching dry down that extended upstream from the lagoons during the drought period.

Of significance for *O. mykiss* in particular, the duration of a breach often exceeded the window of possibility when there was sufficient depth for either returning anadromous adults or emigrating smolts. Adequate depth is necessary to allow for *O. mykiss* passage, with a minimum 0.305 m required for anadromous adults and 0.152 m required for migrating juveniles (Flosi and Reynolds 2010). Sustaining adequate depth for migration of *O. mykiss* both in and out of a creek system is a key factor that needs to be taken into consideration when restoration planning occurs for a lagoon in the Santa Monica Bay.

Southern steelhead trout life history cycles require three important habitat conditions: connection from the ocean into the lagoon, suitable lagoon conditions for smolts to transition from freshwater to saltwater (Bond et al. 2008), and connection from the lagoon upstream to upper creek habitats allowing passage for both smolts and anadromous adults (NMFS 2012). Recovery of this species relies upon all of these elements being functional simultaneously in numerous coastal streams. Connectivity both to the ocean and upstream was extremely limited during the study. Depths measured in these lagoons were on the lower limit of the preferred ranges for supporting smolt growth or transition within the lagoon itself, and the limited wetland and transitional habitat in most of these locations provide limited support for smolts.

The observed ability of larger lagoons in our study area to retain water through the summer and into the following water year has important implications for *O. mykiss* smolts. Smaller smolts with an average fork length of 112 mm were found to stay in a central coast estuary and wait until the following winter to emigrate when they were much larger (Bond et al. 2008). Smolts would not have this opportunity in the smaller lagoons in the Santa Monica Bay, as Arroyo Sequit, Solstice, and Las Flores lagoons dried down to uninhabitable levels as the study period progressed into summer 2017. Data examining the average fork length of smolts in Topanga Creek indicate that most emigrating smolts are larger than 170 mm (Bell et al. 2011), which suggests that environmental cues in the Santa Monica Bay may favor larger smolt sizes for emigration. Even with adequate surface water remaining present throughout the summer in lagoons like Big Sycamore, Topanga, Trancas, and Zuma, connection to upstream habitat was cut off very early in the dry season, between May and June. This phenomenon had been observed consistently in Topanga Creek for many years (Dagit et al. 2017). The lower reach of Topanga Creek has been drying down earlier each successive year of drought, with the length of reach dry also increasing each year.

Previous habitat assessment and barrier identification work in the Santa Monica Bay documented watershed size and geomorphology, both natural and anthropogenic fish passage barriers and habitat quality (CalTrout 2006). Based on an integrated assessment of these factors, CalTrout (2006) prioritized restoration actions to focus on recovery of *O. mykiss.* Their recommended ranking prioritized Topanga, Arroyo Sequit, Trancas, Big Sycamore, Zuma, Las Flores and Solstice. Our study builds on that effort by providing both qualitative and quantitative data on the evolution of breaching and lagoon conditions. Based on the results of this study, the unique challenges and constraints of each system are discussed, with ranking based on all of the above metrics, as well as documented presence of *O. mykiss* since 2000 (RCDSMM unpublished data).

Because it has the best average habitat quality and the third largest habitat quantity in kilometers, as well as supporting the only reproducing population of *O. mykiss* remaining in the Santa Monica Bay, restoration of Topanga lagoon is considered to be the highest restoration priority. Topanga lagoon's unique system sustains a steady pool of surface water throughout the year despite interrupted flow upstream in the low gradient reach during the dry season. The Topanga watershed has a high water table relative to the creek and receives groundwater recharge in most reaches of the creek throughout the entire year (Tobias 2006). The Topanga Canyon rain gauge (#318) measured 11.73 cm of rainfall from October- December 2016, which was sufficient to breach the lagoon on 21 December 2016, but the breach was not sustained. Another 6.91 cm fell before the lagoon breached again on 11 January 2017. With an additional 42.11 cm of rain between January and February, Topanga Lagoon remained breached for a total of 132 d. It was the longest breach period for a larger surface area lagoon in this study and included an estimated 30 d of passable connection. The berm closed on 16 May 2017 and remained closed for the remainder of the study period.

Topanga Lagoon is constrained on all sides by fill slopes, and PCH bridge abutments, which laterally constrain the lagoon's physical features. This caused quicker and longer breaches than might have historically occurred, since the lagoon is not able to expand and spread out naturally to take up a larger surface area and volume.[4] Topanga Lagoon consistently maintained surface water throughout the drought period and required the second smallest amount of rain to breach in the 2017 water year. Tidewater gobies (*Eucyclogobius newberryi*) are supported in this lagoon, and while in-stream vegetation is limited to a small patch on the east side of the lagoon downstream of PCH, these are two potential food sources for smolts.

Restoration that removes constraints on the sides of the lagoon above and below PCH would allow more area for important wetland and transitional upland bank vegetation in addition to potential for sea level rise accommodation. This must be balanced by preserving enough thalweg constraint to continue maintaining a breach. Careful analysis of breach flows needed to connect to the ocean, while expanding the duration of suitable flows that support fish migration will be needed. During the 2017 water year, two anadromous adults entered the system and one of them is confirmed to have spawned (RCDSMM unpublished data). Recent genetic analysis indicates that anadromous genes in this population are currently present, retaining the potential to produce anadromous individuals despite years of limited passage opportunities and purely residential spawning (RCDSMM unpublished data). Restoration planning was initiated in 2004 with the preparation of required documents for replacing the PCH bridge, which continues to date.

Removal of three fish passage barriers in Arroyo Sequit in 2016 restored access to four kilometers of high-quality spawning and rearing habitat for *O. mykiss*, which was utilized by two anadromous adults in January 2017. Arroyo Sequit lagoon saw variable conditions throughout the drought period between 2013 and 2016, with consistent pooling under the PCH bridge associated with a high water table in that area. This relatively small watershed (31 km^2) receives no imported water and is sustained only by groundwater flows from the upper watershed. The lagoon pool was not connected either upstream to the dry creek channel or downstream to the ocean except for one day on 29 October 2015 following a storm. The lagoon had ponded surface water during the winter of 2016, as well as in September-December 2016. After a combined 18.92 cm of rain fell from October-December 2016, the first breach occurred on 20 December 2016. The breach closed for a brief period from 15-17 January 2017 but re-connected following a storm and remained breached through a combined 40.51 cm of rainfall over the following three months. Arroyo Sequit's breach closed on 9 April 2017, but the lagoon remained subject to input daily with high tide overwash through the end of June 2017. The lagoon was breached for a total of 97 d with an estimated 51 d of passibility. Schools of stripped mullet (*Mugil cephalus*) and Topsmelt (*Atherinops affinis*) were documented in the lagoon but were not able to survive as the depth decreased to less than 30 cm (RCDSMM unpublished data). There are no proposals to make any changes to the lagoon at this time.

In Trancas, the grade and concrete pylons/walls at the PCH bridge severely constrain the lagoon, and a channelized portion of the creek just upstream of the lagoon likely contributes to its current tendency to funnel water to the west side of the lagoon, aiding in a quicker breach. The current configuration of the PCH bridge severely limits the ability of the lagoon to move as the bridge pylons redirect flow in a way that has built up sediment on the eastern side of the lagoon. Surface area of Trancas lagoon was in the mid to high range in our study, but also sustained a long breach period. The Trancas Lagoon Restoration Feasibility Study (Dagit et al. 2015) analyzed lagoon restoration alternatives to better understand these relationships and found that there were significant trade-offs between increasing lagoon and wetted area versus increasing or maintaining breach frequency. A larger lagoon footprint decreased the potential for breach, but in the face of sea level rise, adequate lagoon size will be necessary to buffer shoreline recession. While there are currently no *O. mykiss* present in this system, there is historic documentation of *O. mykiss* caught in the 1980's (CalTrout 2006), the upstream habitat is good to excellent and most of the watershed is owned and managed by the National Park Service.

Trancas lagoon experienced brief breaches during the 2014-2015 (5 d) and 2015-2016 (1 d) water years. From October-December 2016, 17.63 cm of rain fell before Trancas lagoon breached on 24 December 2016. The breach was sustained as other storms dropped another 14.86 cm of rain from 30 December 2016 through 12 January 2017. The lagoon closed on 12 January 2017 but reopened again 8 d later with a new storm on 19 January

2017. The breach then remained connected until 18 April 2017, at which time the lagoon closed for the remainder of the water year. Trancas lagoon was breached for a total of 110 d and passable for an estimated 61 d. The berm continued to build vertically as ponded water remained within the lagoon and under the PCH bridge through the end of the water year. Grooming of the berm by LA County Department of Beaches and Harbor occurred immediately after the breach ended.

Restoration of Trancas lagoon is in the planning stages associated with the pending replacement and expansion of the PCH bridge. This process is complicated by both landowner reluctance on the north side of PCH and the proposed re-nourishment of Broad Beach along the ocean. This project could potentially expand the width of the beach berm to almost 60 m, approximately twice its current width. Finally, the upstream concrete trapezoidal flood control channels identified as the keystone passage barrier to the approximately 10 km of upstream habitat are being studied to potentially restore a natural bottom that could facilitate fish passage opportunities.

At Big Sycamore lagoon, both the PCH bridge at the ocean and a pedestrian bridge over the upper end of the lagoon connected by fill slopes on both sides entirely constrain the lagoon area. Waves actively deposit sand under the PCH bridge, creating a vertical berm that inhibits connectivity. The water is thus forced upstream above the pedestrian bridge and into the mainstem of the creek. Substantial vegetation lines the banks above the pedestrian bridge but no vegetation is present either in the lagoon or on the banks of the lagoon between PCH and the pedestrian bridge. The extent of the berm is exacerbated by the concrete walls flanking the PCH crossing. Waves are able to deposit sand, but removal processes are hindered by the southern wall. Big Sycamore was ranked second in total habitat score for the Santa Monica Mountains (CalTrout 2006), but since then the Springs Fire in 2013 devastated much of the upper watershed and subsequent mudslides and sediment deposition further degraded the habitat (NPS pers communication). Regrowth and improvement has occurred, and the 2017 water year showed promise in Big Sycamore creek, but access upstream 19 km to the limit of anadromy was minimal. The lagoon filled and a large reach of the creek upstream remained wetted well past the rainy season. There are currently no *O. mykiss* in this watershed.

Big Sycamore lagoon completely dried down during the 2013-2016 drought period, with occasional puddles appearing in the lagoon due to sporadic overwash or a small rain event. In December 2016, the Lechuza rain gauge recorded 13.13 cm of rainfall, but Big Sycamore lagoon remained disconnected from the ocean. It was not until another 28.37 cm of rain fell over two storm events that the lagoon finally breached on 23 January 2017. After 5 d of connection, the berm closed, but was reopened one week later with another series of rain events that totaled 24.38 cm over a 31-d span. Despite this large amount of rainfall in the watershed, Big Sycamore lagoon closed on 8 March 2017. Small rain events in March and April 2017 were unable to cause another breach; the berm remained intact for the remainder of the year. An estimated 39 d of breach were recorded, the minimum for our entire dataset, with only 30 d of passable connection, most often at times of high tide. Once closed on 8 March 2017, the berm began to substantially build up.

The PCH–pedestrian bridge complex has been identified as the keystone passage barrier in this system and has recently been placed on the priority restoration list by Caltrans District 7 (Caltrans pers. communication). Efforts are underway to obtain funding for the feasibility study needed to examine overall watershed processes post fire and develop a restoration plan.

The restoration challenges at Zuma lagoon are exacerbated by over 20 fish passage barriers extending from the Zuma Beach driveway and Arizona crossing, upstream through numerous private properties to the public area owned by National Park Service.[10] Planning has been in progress since 2005 to replace the Arizona crossing with a bridge, and to restore passage under PCH, but implementation funding is still missing. NPS restored over five acres of tules and transitional upland vegetation on the east side of the lagoon in 2010, but management for mosquito abatement resulted in creation of paths through the tules that has fragmented that habitat and attracted transients.

Habitat quality in Zuma lagoon was documented prior to the drought. Despite the added natural wetland vegetation, high water temperatures, dissolved oxygen level limitations, and extensive eutrophication would make this a challenging habitat for *O. mykiss* (McLaughlin et al. 2014). Zuma lagoon almost completely dried down during the 2013-2016 drought period and did not breach at all. Only a small fraction of the lagoon area had surface water in October and November 2016. It took a combined 42.09 cm of rainfall from October-January for Zuma lagoon to breach on 20 January 2017. Two more large rain events, with a combined total of 29.49 cm of rainfall recorded, sustained the breach for a total of 41 d with 39 d of passibility into the lagoon, dependent on high tide conditions. Once rain events ceased, the lagoon closed on 1 March 2017 at very high-water capacity, and the 200 m wide berm seen at this location built back up rapidly. Grooming and beach manipulation by LA County Department of Beaches and Harbors, who maintain the berm closure to provide lifeguard vehicle access across the beach, assisted in the rapid berm buildup.

Almost all the upstream fish passage barriers in Solstice have been removed during the past decade by the city of Malibu and National Park Service. The final constraint is a Caltrans box culvert under PCH that has been the subject of much restoration analysis for years; it creates a steep >1 m drop-off with no jump scour pool that precludes fish passage during much of the breach period. Final planning for a bridge to replace the culvert is in progress but there is no current timeline for implementation. While there is historic documentation of *O. mykiss* in Solstice (Dagit et al. 2005; NMFS 2012), lagoon development and presence is currently ephemeral and constrained by PCH and houses. Sometimes there is kelp washed up to the pool, but otherwise there is no vegetation and habitat is marginal at best. Flow through the culvert rarely exceeds 5 cm depth, although riparian cover and suitable habitat is available from the upstream end of the culvert to the limit of anadromy approximately three kilometers upstream.

Solstice lagoon experienced breaches in the 2014-2015 (7 d), and 2015-2016 (11 d) water years. During 2016-2017, the first breach occurred on 23 December 2016 after a combined 14.73 cm of rain fell from 1 October 2016 through the day of first breach. With an additional 49.02 cm of rain recorded over the 2017 rainy season, the breach remained connected until closure on 4 July 2017. Solstice lagoon remained open for the longest period out of all the locations in our study area but was completely impassable. When the breach was first initiated, there was a short window before enough sand had washed away that would have allowed passage from the ocean to the culvert, but not further upstream. Subsequent sheet flow across the beach face and the smooth concrete bottom of the culvert also restricts passibility. Additional human interference was a constant occurrence at this location. Sandbags were found within the culvert and obvious trenches appeared dug into the sand to divert flow.

---

[10] Kelley, E., E. Wallace, and M. Stoecker. 2013. Southern California steelhead recovery and barrier removal recommendations for Zuma Creek, Santa Monica Mountains National Recreation Area. Prepared for Santa Monica Mountains Foundation and the Southern California Research Learning Center, Thousand Oaks, CA.

Although Caltrout (2006) and NMFS (2012) recovery plan both identify Las Flores as having potential *O. mykiss* habitat, there is no historic record of fish in this system and the anthropogenic constraints at the beach pose significant barriers. Las Flores lagoon has an extremely constricted channel bordered by concrete walls on either side both up and downstream of the PCH bridge, which funnels flows to the beach. Due to the fire hose funneling effect of these constraints, it breached every year despite drought conditions in the 2013-2016 water years. These breaches were variable in length, lasting 4, 10, and 7 d, respectively. A combined 16.51 cm of rain fell from 1 October 2016 until the first breach occurred on 24 December 2016. The breach was sustained throughout the rest of the rainy season, with an additional 39.12 cm of rain recorded, until its closure on 22 April 2017. Total breach time in 2017 equaled 119 consecutive days with an estimated 44 d of passibility into the lagoon but the lack of connected surface flow in the upstream channel precluded any further movement. Berm buildup occurred over the month of May 2017, and at the end of the 2017 water year what remained of the lagoon sat dry, 1-3 m below the height of the completely closed off berm.

In addition to the site-specific constraints found at each lagoon system, the global effects of sea level rise also need to play a role in developing restoration scenarios. According to a Los Angeles County Public Beaches Sea Level Rise Vulnerability Assessment (Noble 2009), most beaches in the western portion of the county are expected to be eroded under a high sea level rise scenario by 2040. Topanga beach is expected to erode completely and Zuma beach is projected to erode by ~70%. By 2100, Zuma beach and Topanga beach are expected to recede by 184 feet and 190 feet respectively. While the other lagoons in our study were not included in the LA County Assessment, we can infer that erosion and recession could be similar under high sea level rise conditions. Explicitly evaluating the ecological trade-offs between ensuring adequate connectivity and increasing transition zone habitat in the face of sea level rise, as well as examining the best way to develop a realistic, self-sustaining mosaic of ecosystem habitat types and services, is necessary but difficult (Southern California Wetlands Recovery Project 2018). Continued monitoring of lagoon volume over time can help inform management decisions by providing accurate knowledge of how a given lagoon responds to rainfall, and how it provides habitat to emigrating smolts and anadromous adults returning to riparian headwaters. It will be critical for managers and restoration planners at all lagoon sites to balance the need for breach connectivity with lagoon footprint as restoration plans move forward.

Conclusions

The recovery of anadromous adult steelhead trout to headwaters of southern California creeks is contingent on open and passable lagoon conditions. Our analysis of lagoons in the Santa Monica Bay indicates that lagoon surface area correlated positively with the amount of rain needed for the first breach to occur but negatively with the number of days a breach persisted. Larger lagoons in our study area tended to open later and close more quickly than smaller lagoons. At the same time, larger lagoon footprints could offer sea level rise protection to estuarian vegetation and other wildlife that is critical to the overall health of the ecosystem (Southern California Wetlands Recovery Project 2018). As observed during the study period, lagoons with smaller footprints have little potential to provide smolt rearing habitat and provide limited anadromous adult passage. At this point in time, all of the lagoons in our study region would be considered unsuitable for rearing smolts. While it has been continually observed that *O. mykiss* smolts do not linger for very long in estuaries[11] (Welch et al. 2004), insufficient lagoon volume can also lead to increased predation risk by birds (Kelley 2008; Osterback et al. 2015). Lagoons with larger footprints have better potential to be utilized as smolt habitat with decreased predation risk since they retained volume the longest through the summer and into the next water year. Adequate depth played a role here, as larger surface area locations were deeper overall, providing habitat that is more protected than shallower areas. The problem is that these lagoons also tend to breach less frequently, restricting anadromous adults from entering to spawn, which can result in fewer fish overall (NMFS 2012).

The last important part of restoring connectivity for *O. mykiss* is for fish to have access from the lagoons upstream to headwater spawning and rearing habitat. Dry down of lower reaches in these creeks poses a significant barrier for both adult and juvenile migration to and from the lagoon. As extensively documented in Topanga Creek, the stream channel dries down from 200 to ~1700 m every summer (Dagit et al. 2017), effectively rendering the lagoon habitat useless to any anadromous adults or smolts that failed to enter the creek or ocean during a short period of passable connection. This pattern was also observed in all the other watersheds. Water temperatures in the study area lagoons consistently reach stressful levels during the summer months and these already high temperatures increased over time (RCDSMM unpublished data). Additionally, instream vegetation, which provides habitat for benthic macroinvertebrates and terrestrial insects, and provides a major food source for juveniles (Krug et al. 2012), is virtually nonexistent in every lagoon of our study area (RCDSMM unpublished data).

The measurements recorded and analyzed in this study provide insight into the volumetric characteristics that small creek archetypal lagoons display in southern California's Mediterranean climate. With the Santa Monica Bay predicted to face more extreme conditions due to climate change and sea level rise, maintaining sufficient volume in the lagoons in our study area as well as managing them to support connectivity will become increasingly more important to the recovery of southern steelhead trout. Unfortunately, due to the small data set with only three points in time measured for each lagoon, robust statistical analysis was not possible to further illuminate the complex dynamics that need to be understood in order to develop self-sustaining long-term restoration plans.

Passage limitations due to drought are a key limiting factor affecting adult steelhead in the Santa Monica Bay, and despite the ability to spawn multiple times anadromous adult movement is hindered by flashy peak flows characteristic of southern coastal streams (NMFS 2012). In both Topanga and Arroyo Sequit, anadromous adults were able to migrate upstream in 2017, despite the short window of opportunity for passage. They were not able to return to the ocean due to low flow conditions in the creeks. If climate predictions for low flow conditions continue and further restrict migration opportunities, *O. mykiss* may have no choice but to remain in freshwater refugia pools. Resident *O. mykiss* are typically smaller and less fecund than ocean-going steelhead (NMFS 2012). The implications of reduced connectivity and migration opportunities could decrease resiliency of southern *O. mykiss* by increasing the risk of local extirpations and restricting genetic flow among neighboring systems (NMFS 2016). As sea level rise is projected to inundate wetland habitat across southern California in the next 100 years (Thorne et al. 2018), now is an opportune time to set up management plans to ensure adequate estuarine and transitional habitat remains resilient in the face of climate change and anthropogenic stressors. This study provides insight into how the lagoons in the study area rebounded from drought conditions and subsequently evolved over a wet period followed by the hot and dry season.

---

[11] Kelley, E. 2008. Steelhead trout smolt survival: Santa Clara and Santa Ynez River estuaries. Report for California Department of Fish and Game Fisheries Restoration Grant Program, University of California, Santa Barbara, CA 61 pp.

With the current population of southern steelhead trout at record lows, the importance of passage opportunities in the Santa Monica Bay are more important than ever. Increased fire risk and uncertain precipitation levels that have come along with climate change will be an important consideration for management in the future as populations have the potential to be completely extirpated during a single natural hazard. Enhancing the ability of southern steelhead trout to move not only within their own watershed, but also between watersheds, could be vital to preserving this population. Finding the balance between lagoon volume and breach potential will be critical.

Acknowledgements

Funding for this effort was provided through a contract with the California Department of Fish and Wildlife Fisheries Restoration Grants Programs number P1450013. Additional thanks to California State Parks Angeles District, Santa Monica Mountains Conservancy, and the Santa Monica Mountains National Recreation Area for providing access. Field work was conducted by RCDSMM Stream Team members including: K. Adamek, A. Balcerzak, B. Chubak, R. Dauksis, J. Mongolo, E. Montgomery, G. Nichols, A. Spyrka, and S. Williams. Watershed Steward Project members B. Dimirci, D. Hofflander, A. Sanchez, and N. Trusso also assisted with field work. This paper greatly benefitted from early review by M. Abramson and Dr. C. Swift, and input by two anonymous reviewers.

Literature Cited

Behrens, D.K., F.A. Bombardelli, J.L. Largier, and E. Twohy. 2013. Episodic closure of the tidal inlet at the mouth of the Russian River: a small bar-built estuary in California. Geomorphology, 189:66–80.

Bell, E., R. Dagit, and F. Ligon. 2011. Colonization and persistence of a southern California steelhead (*Oncorhynchus mykiss*) population. BSCAS, 110(1):1–16.

Bond, M.H., S.A. Hayes, C.V. Hanson, and R.B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Can. J. Fish. Aq. Sci., 65:2242–2252.

Cooper, J.A.G. 2001. Geomorphological variability among microtidal estuaries from the wave-dominated South African coast. Geomorphology, 40(1-2):99–122.

Dagit, R., E. Bell, K. Adamek, J. Mongolo, E. Montgomery, N. Trusso, and P. Baker. 2017. The effects of prolonged drought on southern steelhead trout (*Oncorhynchus mykiss*) in a coastal creek, Los Angeles, California. BSCAS, 116(3):162–173.

Day, J.H. 1980. What is an estuary. S. African J. Sci., 76(5):198–198.

Elwany, M., S. Hany, R.E. Flick, and S. Aijaz. 1998. Opening and closure of a marginal southern California lagoon inlet. Estuaries, 21(2):246–254.

FitzGerald, D.A., 1996. Geomorphic variability and morphologic and sedimentologic controls on tidal inlets. J. Coastal Research, 23:47–71.

Kraus, N.C., K. Patsch, and S. Munger. 2008. Barrier beach breaching from the lagoon side, with reference to Northern California. Shore and Beach, 76(2):33–43.

MacDonald, J., C. Levings, C. McAllister, U. Fagerlund, and J. McBride. 1988. A field experiment to test the importance of estuaries for chinook salmon (*Oncorhynchus tshawytscha*) survival: short-term results. Can. J. Fish. Aq. Sci., 45:1366–1377.

McLaughlin, K., M. Sutula, L. Busse, S. Anderson, J. Crooks, R. Dagit, D. Gibson, K. Johnston, and L. Stratton. 2014. A regional survey of the extent and magnitude of eutrophication in Mediterranean estuaries of Southern California, USA. Estuaries and Coasts, 37(2):259–278.

McSweeney, S.L., D.M. Kennedy, and I.D. Rutherfurd. 2017. A geomorphic classification of intermittently open/closed estuaries (IOCE) derived from estuaries in Victoria, Australia. Progress in Phy. Geo., 41(4):421–449.

Nerem, R.S., B.D. Beckley, J.T. Fasullo, B.D. Hamilington, D. Masters, and G.T. Mitchum. 2018. Climate-change-driven accelerated sea-level rise detected in the altimeter era. PNAS 115(9): 2022–2025.

National Marine Fisheries Service (NMFS). 2012 Southern California Steelhead Recovery Plan. Southwest Regional Office, Long Beach, CA.

———. 2016. 5-Year review: summary and evaluation of southern California coast steelhead distinct population segment. National Marine Fisheries Service. West Coast Region, California Coastal Office, Long Beach, CA.

Osterback, A.K., D.M. Frechette, S.A. Hayes, S.A. Shaffer, and J.W. Moore. 2015. Long- term shifts in anthropogenic subsidies to gulls and implications for an imperiled fish. Bio. Cons., 191:606–613.

Rich, A, and A, Keller. 2012. Watershed controls on the geomorphology of small coastal lagoons in an active tectonic environment. Estuaries and Coasts 35:183–189.

Thorne, K., G. MacDonald, G. Guntenspergen, R. Ambrose, K. Buffington, B. Dugger, C. Freeman, C. Janousek, L. Brown, J. Rosencranz, J. Holmquist, J. Smol, K. Hargan, and J. Takekawa. 2018. U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. Sci. Adv., 4:eaao3270.

Tobias, V. 2006. Groundwater sources and their influence on the distribution of steelhead in Topanga Creek, Topanga, California. Master's Thesis. University of Michigan, Ann Arbor.

Welch, D.W., B.R. Ward, and S. Batten. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. Deep-Sea Research II, 51:897–909.

Bull. Southern California Acad. Sci.
118(3), 2019, pp. 200–201

Obituary

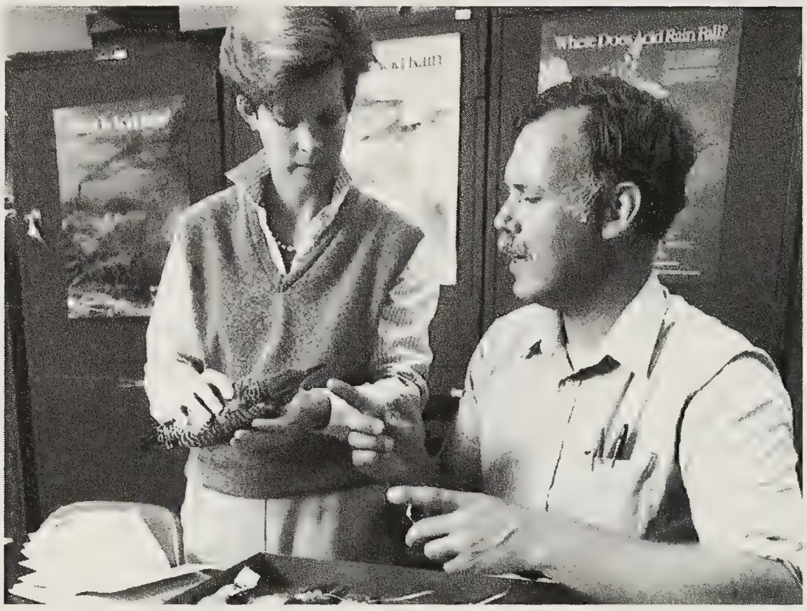


Image: Claremont McKenna College

Long-time SCAS Fellow and Professor of Biology Emeritus at Claremont McKenna College Daniel Guthrie died on July 1, 2019.

Guthrie, 80, specialized in comparative anatomy, animal behavior, introductory biology and environmental science during his 48 years at the Claremont Colleges, and had a lasting impact on students interested in careers in biology, ecology and medicine. Guthrie was an active member of SCAS in which he served as secretary, treasurer and Bulletin editor, and whose contributions to the academy's mission are unprecedented.

Dan authored more than 70 papers and studies in biology, and led innumerable field trips both locally and abroad. Every summer the Guthrie family drove across the United States, camping, looking at birds and collecting fossils. One of his favorite yearly expeditions was to San Miguel Island, which is one of the most remote destinations amongst California's Channel Islands. He also had an extensive collection of seaweed that he gathered from Alaska's Aleutian Islands while birding on Attu Island. His love for learning never faded, which inspired his travels to more than 40 countries, including Madagascar, Mongolia and Belarus.

Born in Terre Haute, Ind. and raised in Garden City, N.Y., Guthrie attended Amherst College, where he studied biology and played lacrosse. He earned a Master's degree in biology from Harvard and a doctorate from the University of Massachusetts. As a biologist, he salvaged and collected U.S. bird skeletons for use by museums and teachers. He donated his time and expertise to finding and identifying fossil bird bones from roads, excavations, and collections for local educational institutions.

Even as his mobility worsened, Dan still got out of the house to watch birds and enter data into Cornell's eBird database. His extensive collection of bird watching notebooks continued through 2019, which included observations of more than 7,000 bird species. Guthrie also loved soccer, attending games at Claremont College, and watching the FIFA Women's World Cup right up to his passing.

SCAS offers the sincerest condolences to Dan's family: daughters Kate Poaster, Ruth Guthrie and Winnie Larson, and their spouses, Bob, Dave Overoye and Tom, respectively; grandchildren Lee, Ben, Bobby, Acacia, Sage, Jack, Teddy and Alex; and great-grandchildren Aydan, Gavyn and Cypress; and to all whose lives and careers were touched by Dan's generosity and influence.

Dave Ginsburg, Ph.D.

SCAS President

SMITHSONIAN LIBRARIES
3 9088 01817 9390

CONTENTS

Experimental Elucidation of the Life Cycle of *Rhinebothrium urobatidium* (Cestoda: Rhinebothriidea) from the Round Stingray (*Urobatis halleri:* Myliobatiformes) to First and Second Intermediate Hosts Ralph G. Appy, Shana K. Goffredi, Bruno Pernet, and Carin Latino 139

Secondary Production of Kelp Bass *Paralabrax clathratus* in Relation to Coastal Eelgrass *Zostera marina* Habitat in a Southern California Marine Protected Area Richelle L. Tanner, Adam K. Obaza, and David W. Ginsburg 158

Temporal and Volumetric Characteristics of Lagoons in the Santa Monica Bay and the Passage Implications for Southern Steelhead Trout Danielle Alvarez and Rosi Dagit 173

Obituary 200

Cover: Dan Guthrie photo with permission of Claremont McKenna College.